The Oxford Handbook of Human Mating

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Edited by

David M. Buss

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Introduction to Human Mating Strategies

David M. Buss

Abstract

In sexually reproducing species, mating success is a non-negotiable requirement for evolutionary fitness. Consequently, selection has created a rich array of adaptations that are products of a long and unbroken line of human ancestors, each of whom succeeded in the complex game of mating. This Handbook showcases the current state of knowledge about those adaptations. These include mate preferences, tactics of attraction, forms of mate competition, tactics for dealing with sexual conflict, modes of mate retention, mate switching strategies, and many more. Chapters on the endocrinology of mating adaptations provide state-of-the-art knowledge about some of the key biological drivers. Chapters on mating in the modern world highlight key ways in which mating adaptations, forged over millions of years in environments long gone, get expressed in modern environments, sometimes creating evolutionary mismatches. This Handbook is not the final word on human mating strategies. Rather, it gives readers and researchers an impressive foundation of what is known and unknown, and importantly, a roadmap for future discoveries about what may be the most complex evolved psychology humans possess.

Key Words: human mating strategies, sexual selection, mate preferences, mate competition, evolutionary mismatches

The scientific study of human mating strategies is one of the major success stories of evolutionary psychology. The explosion of evolutionarily anchored theories and thousands of empirical studies of human mating is unique among the social sciences in at least two respects—the volume of hypothesis generation and the cumulative quality of the scientific empirical testing. This makes good theoretical sense. In all sexually reproducing species, evolutionary processes must all pass through the rigorous filters of successful mating. Survival is not

enough. Each living human comes from a long and literally unbroken chain of ancestors, each of whom succeeded in selecting a mate, attracting a mate, being reciprocally chosen by that mate, navigating the complexities of sexual intercourse sufficient for conception, having a conceptus who survived the nine-month hurdles to be born, and after birth survived to reproductive age to begin the process anew.

Passing through these successive hurdles had to happen not just a dozen times but millions upon millions of iterations going back through the distant mists of human evolutionary history, our primate lineage, our mammalian lineage, and the origin of sexual reproduction itself more than a billion years ago. If any one of our ancestors had failed in any of these tasks, the chain would be irreparably broken and we would not be alive to read these pages. In this important sense, we are all evolutionary success stories. As descendants of this unimaginably long line of forbears, each us carries with us the finely honed adaptations that led to our ancestors' success. The current *Handbook of Human Mating* provides an up-to-date summary of the current state of the science of human mating—the modern theories, hypotheses, predictions, and empirical findings relevant to each.

Sexual Selection Theory

Sexual selection theory (Darwin, 1871) provides the most important theoretical framework for understanding the mating adaptations of sexually reproducing species (e.g., Andersson, 2019). Sexual selection centers on the evolution of adaptations not due to survival success but rather due to mating success. Darwin identified two causal processes by which mating success could be attained—intrasexual competition and preferential mate choice. The classic example of intrasexual competition is two male stags locking horns in combat. Winners in these physical contests gained preferential sexual access to females, and so passed on genes for attributes that led to their success such as greater strength, agility, speed, and perhaps fearlessness and bellicosity. The attributes of losers bit the evolutionary dust because they failed in this brutal game of mating. Contest competition turns out to have been an extremely important sexually selective process in humans (Puts et al., this volume).

The second process of sexual selection articulated by Darwin identified the evolution of mating success through preferential mate choice. If members of one sex preferred certain qualities in the other sex in mating contexts, then those who possessed the desired qualities were more frequently chosen. Over evolutionary time, if there exists some degree of consensus about the qualities desired and

those qualities are partly heritable, then the desired qualities evolve or increase in frequency.

Although Darwin envisioned intrasexual competition as pertaining primarily to males and preferential mate choice pertaining primarily to females, when it comes to humans, both processes apply to both sexes, as the chapters in this *Handbook* document. Moreover, the modes of intrasexual competition in humans involve not just physical contests, although it's clear that these have been important. Rather, arenas of intrasexual competition include tactics for navigating status hierarchies and the use of language to influence social perceptions of one's own mating desirability and to impugn the reputation of intrasexual rivals (Buss & Dedden, 1990; Fisher & Krems, this volume).

Sexual selection theory itself has witnessed important theoretical developments since Darwin's 1871 articulation of it (see Ryan, this volume). Trivers (1972), for example, furnished a major theoretical advance by identifying the relative parental investment of each sex as a key determinant of which sex does the competing and which sex does the choosing (see Trivers, this volume, on the personal context in which he developed his theory). Sexual selection theory has also expanded to include processes such as sperm competition (Starratt & Shackelford, this volume) and sexual coercion (see Camilleri, this volume).

The chapters in this volume showcase the "state of the art" of sexually selected human mating strategies and the underlying psychological adaptations that give rise to them.

Sexual Conflict Theory

Another critical theoretical development since Darwin's time has been sexual conflict theory (Parker, 2006; Perry & Chapman, this volume). When the genetic interests of females and males diverge, sexual conflict will ensue. There exist many domains of sexual conflict in humans, zones in which the optimal mating strategy from a female perspective differs from the optimal mating strategy from a male perspective. It is sometimes in a male's best interest to initiate sex sooner, or with less investment, compared to the optimal interests of the female. These differing fitness interests create sexually antagonistic arms races very much analogous to those that occur between predators and prey. Each sex evolves adaptations to influence the other to be closer to its own optimum, which creates counteradaptations or defenses in the other to resist that influence and to manipulate the other sex to closer to its own optimum. This form of sexually antagonist evolution is often perpetual.

The many chapters on sexual conflict in this volume highlight the theoretical utility of sexual conflict theory in guiding researchers to discoveries that were entirely unknown prior to this theoretical development. These include predictable forms of deception in mating (Brewer, this volume), infidelity and jealousy (Scelza, this volume), adaptations for sperm competition (Starratt & Shackelford, this volume), intimate partner violence (Duntley, this volume), various forms of sexual coercion (Brown, this volume; Camilleri, this volume) as well as women's defenses against sexual coercion (James et al., this volume).

Sexual Strategies Theory

Social scientists, including psychologists, typically receive no training in evolutionary biology. Consequently, most were unaware of these key theoretical developments in evolutionary theory and their potential applicability to human mating. In the last half of the 1980s and early 1990s, this started to change. Cunningham (1986) launched experimental tests of the evolution of female beauty from an evolutionary perspective. Kenrick et al. published a paper documenting that social dominance increased the attractiveness of men as mates but did not increase the attractiveness of women (Sadalla et al., 1987). And Buss (1989) published the first large-scale cross-cultural tests of evolutionary hypotheses about sex differences in human mate preferences.

The first major attempt to develop a more comprehensive evolution-based psychological theory of human mating strategies came under the rubric "sexual strategies theory" (Buss & Schmitt, 1993). This theory, containing nine key premises and twenty-two empirical predictions, proposed that humans have evolved a menu of mating strategies, not a single mating strategy. It provided a task analysis of the different adaptive problems that women and men recurrently face in mating, cross-cut with the temporal dimension of short-term mating (e.g., casual sex and brief affairs) and long-term mating (e.g., marriage and other temporally enduring mating relationships). It proposed that women as well as men engage in short-term mating, but the adaptive challenges they face when pursuing this strategy differ profoundly. The reproductive benefits to men of pursuing a short-term mating strategy are fairly straightforward, since men's reproductive success is most heavily limited by the number of fertile sex partners they can attract. Consequently, sexual strategies theory predicted that men would desire a larger number of partners than women do, let less time elapse before seeking sexual intercourse, and possess a host of other psychological design features that would promote the success of a short-term mating strategy (e.g., the male sexual overperception bias, first predicted by Buss, 1994).

Although women generally cannot (and never could) increase their direct reproductive success through short-term mating since adding additional sex partners would rarely have resulted in more offspring, they could use short-term mating to obtain key adaptive benefits. According to sexual strategies theory, these might include (1) immediate access to resources, (2) assessing several men through trial runs to determine which would be a good long-term mate, (3) cultivating a backup mate for insurance should something go wrong with her long-term relationship, (4) using short-term mating as a tactic for "trading up" to a higher mate value partner, and perhaps (5) obtaining higher-quality genes (e.g., genes for good health) from an affair partner than she could obtain from her regular partner. In the intervening years since the publication of sexual strategies theory in 1993, a tremendous volume of research has focused on testing hypotheses and predictions based on these theoretical benefits (e.g., Greiling & Buss, 2000, on women's perceptions of the benefits of short-term mating; Buss et al., 2017 on the mate-switching hypothesis; Gangestad et al., this volume, on the good genes hypothesis).

Sexual strategies theory also provided a task analysis of the adaptive challenges each sex faces when pursuing a long-term mating strategy. Women, for example, were hypothesized to face challenges such as (1) identifying men who are *able* to invest in them and their offspring, (2) identifying men who are *willing* to invest in them and their offspring, (3) identifying men able and willing to protect them (e.g., from sexual aggression from other men), (4) assessing men who give cues to long-term commitment to them, and (5) assessing men who give cues to "good dad" qualities linked with parenting skills. Men, while facing some of these adaptive challenges in selecting their mates for long-term mating such as commitment and good parenting, also had to solve additional sex-differentiated ones: (1) choosing women likely to be sexually faithful, thus solving the problem of paternity uncertainty (stemming from the fact that fertilization occurs internally within women), and (2) identifying women of high reproductive value (i.e., future reproductive capacity).

Since the 1993 publication of sexual strategies theory, a large body of empirical evidence has accumulated that supports many of the specific predictions generated by it (see Buss & Schmitt, 2019, for a review). Moreover, sexual strategies theory has been extended in new directions to include testing hypotheses across peoples, cultures, and ecologies (see Schmitt, this volume).

In this *Handbook*, multiple chapters showcase important theoretical developments and novel empirical extensions of the scientific understanding of human mating strategies. In the section "Attraction and Mate Selection," Li and his colleagues outline the logic and evidence of strategies in the early stages of

mate selection. Conroy-Beam provides a novel computational model of mate selection that yields a sophisticated way of viewing the multidimensional process of mate selection. Lewis and colleagues provide a “state of the science” summary of theory and research on physical attractiveness using a cue-based approach. Lieberman and Patrick discuss theory and research on incest avoidance adaptations. Apostolou presents arguments and evidence for the importance of parents in influencing, and in some cases selecting, the mates of their daughters and sons. Schacht and Uggla highlight the importance of sex ratio, which surely varied tremendously across cultures and over time, on the mating strategies people pursue.

Kennair and colleagues discuss mating strategies in sexually egalitarian cultures such as Norway. Although some theories, such as traditional sex role theory, predict that sex differences should diminish or vanish in sexually egalitarian cultures, the data do not support those predictions. Indeed, some sex differences become larger, not smaller, in sexually egalitarian cultures. The concluding chapter in this section, by Frederick and colleagues, summarizes what is known about mating strategies as a function of individual differences in sexual orientation such as gay men, lesbian women, and bisexual individuals.

Pair-Bonded Relationship Dynamics

Once mate selection and mate attraction processes have been successfully implemented, complex dynamics occur within those who form long-term pair-bonded mating relationships. Birnbaum examines the role of attachment within pair-bonds. Jankoviak and colleague articulate the importance of love as universal phenomenon within long-term mateships. Meltzer explores the determinants of marital and sexual satisfaction within relationships. Edlund and colleagues examine the importance of jealousy within mateships, which some have argued is as central as love in human mating (Symons, 1979). Jealousy is an emotion often tied to mate guarding, the subject of the final chapter in this section, written by Starratt and Shackelford.

The Endocrinology of Human Mating

All mammals have complex endocrine systems that influence, and are influenced by, mating, and humans are no exception. These are sex-differentiated to an important extent. Reproductive-age women who are not on hormonal contraceptives, for example, experience predictable endocrinological changes as

they progress through their ovulatory cycle. Roney kicks off this section by providing a broad overview of the state of the science on hormones and human mating. However, there is currently scientific controversy about the effects of the ovulation cycle on women's mating strategies. Gangestad and colleagues argue that women possess a "dual mating strategy," suggesting that women have not "lost estrus" as many have argued, and moreover show preference and other mating strategy shifts depending on whether the odds of impregnation are high or low. Sterns and Penke, in contrast, argue that the cycle-phase shifts are more ephemeral or absent, according to large-scale attempts at replication. Resolution of this ongoing debate must await further research within this vibrant and cutting-edge area of the evolution of human mating. Concluding this section is a lively chapter by Cunningham and Hill who summarize the evidence on the effects of modern hormonal contraceptives on women's sexuality and mating psychology.

Mating in the Modern World

The final section of the *Handbook* explores mating in the modern world, which has changed dramatically from the environment in which humans spent 99 percent of their evolutionary history. Helen Fisher and Justin Garcia explore mate choice in the digital age, with the dramatic surge in online dating and mating. Salmon and Burch examine popular culture in the modern world, including pornography, romance novels, and literature. Concluding this section is a chapter by Goetz, who outlines a number of key "mismatches" between the mating environments in which humans evolved and those they now inhabit.

I hope this *Handbook* provides a key reference for researchers and budding scientists who devote their efforts to uncovering the complexities of human mating. Biologist Theodosius Dobzhansky famously noted that "nothing in biology makes sense except in light of evolution." It may not be too far a stretch to say that "nothing in human behavior makes sense except in light of human mating."

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PART I

Theoretical Perspectives

CHAPTER
1

Writing Trivers's 1972 Theory of Parental Investment and Sexual Selection

Robert Trivers

Abstract

A brief summary of the most wide-ranging paper of mine, covering the evolution of sex differences in all species. Especially novel is the application to differential mortality by sex, which varies widely across species and higher taxa. The paper provided a framework, anchored in sexual selection and parental investment, for discovering and explaining many sex differences in human mating strategies. The paper has become one of the most widely cited publications in evolutionary biology, accruing more than 17,000 scientific citations as of the year 2022. It is also one of the most widely cited papers in the mushrooming field of evolutionary psychology.

Key Words: Robert Trivers, parental investment, sexual selection, sex differences, mating

I have described in print and in detail (Trivers 2002) how I came to write this chapter so I will not go into great detail now. There were three parts: pigeon behavior (Drury), key logic (Mayr, Bateman, 1948), and also valuable sublogic (Williams). Were pigeon couples really monogamous with no internal conflict (ornithology); nonsense (Drury, personal communication, date); what was the underlying logic (parental investment (Bateman, 1948; Mayr) and sublogic (Williams, 1966).

The first was to see that the conflict-free monogamous bird family was a fantasy of bird scientists, supported by neither evidence nor logic. All you had to do was watch an actual bird couple—up close and personal—and you could see

the truth. Why would a male force his partner (for life) into sleeping on the sloping roof every night instead of the gutter, where all the other pigeons slept including himself? Does it have anything to do with the fact that in the gutter next to her would be another "monogamous" *male* sitting close to *his* partner? It was Bill Drury who taught me this entire approach. And Bill did not joke around. When I invented a patently nonfunctional explanation for the function of a gull trait we were observing—side by side with binoculars—he told me "Never assume the animal you are studying is as stupid as the one studying him." I was that stupid animal. Here is a more extensive description of Bill Drury and what he meant to me (Trivers 2002):

"Go Thou to the Pigeon"

After I had spent a year or so watching herring gulls and other sea birds with Bill Drury, I wanted to start a project on a species of my own, a species that I could study on land. I believe I suggested the lesser marsh wren, so to speak—that is, a species whose social behavior and ecology had not yet been studied, though something would be known about a closely related species. Drury immediately batted down that idea. He said it would take me eighteen months to find the species on a regular basis and another eighteen months to acclimate individuals sufficiently to me to permit detailed behavioral observations. That it had not yet been studied, he said, might better be taken as a warning than as an invitation. He suggested I go in the other direction—study the pigeon, he said. They were everywhere in Cambridge and too ugly (due in part to earlier domestication) and common to attract any ornithologist since a monograph by Whitman (1919). The variability in feather patterns that helped make them ugly also made individuals easy to identify, so behavioral observations of known individuals could begin right away without the need to capture and handle the birds. As it turned out, at the North Cambridge third-floor apartment where I was living, there were in fact pigeons that roosted on the roof of the house next door that could provide a steady stream of behavioral observations right through the night!

What soon became clear in this monogamous species was that males were sexually much more insecure than were females, and males acted to deprive their mates of what they would be perfectly happy to indulge in themselves, that is, an extra-pair copulation. For example, the group outside my window began with four pigeons—two mated couples. They slept next to each other in the gutter of the roof of the house next door. They often settled on the roof any time after four o'clock in the afternoon. When spending the night together as a foursome, the

two males, although they were the more aggressive sex, always sat next to each other with each one's mate on the outside. By sitting next to each other, the males could ensure that each one was sitting between his mate and the other male.

Then, for a period of several days, a new male arrived and was regularly attacked by each of the two resident males and driven off. Finally, after four or five days of persistence, such a male might still be sleeping twenty yards down the gutter from the other four pigeons, and subject to attack without notice. The very day he arrived with his own mate, however, the distance to the other birds was cut in half, suggesting that male concern about male visitors might be associated with some sexual threat or increased chance that his mate would indulge in an extra-pair copulation. More striking still, when the third couple managed to join the other two, it was no longer possible for each male to sit between his own mate and all other males. What happened then was that the outermost males kept their mates on the outside, thus sitting between their mate and the other two males, but the innermost male forced his female onto the sloping roof in front of them, rather than allow her to sit between him and his neighbor to the right! The female was not happy with this situation and would return to the more comfortable (and warmer) gutter, only to be forced back onto the sloping roof. Sometimes she would wait for him to fall asleep and would slip down beside him unnoticed, but I would soon hear roo-koo-kooing out my bathroom window and would rush to see her pushed back onto the roof. This, for me, was a surprising observation because it put the lie to the notion, so common in ornithology and evolutionary thinking at the time, that the monogamous relationship was one without internal conflict. Here was a male willing to force his own mate, mother of his offspring-to-be, up onto the sloping roof all night long because of his sexual insecurities. This suggested relatively strong selection pressures.

Whitman (1919) reported a sex difference in behavior upon viewing the partner in adultery that I thought was instructive along these same lines. Whitman said that when a male pigeon saw his female about to begin copulating with another male, he flew straight at the second male, attempting to knock him off her; that is, he interrupted the copulation as soon as possible. By contrast, a female seeing her own mate involved in the same behavior would not attempt to stop the copulation but would intervene immediately afterward, separate the couple, and act to keep the other female away from her mate. What was going on here? The obvious answer was suggested by the relative investment of the two sexes in the offspring, certainly at the time of copulation. The male's investment at copulation is trivial, or relatively minor, but the female's investment may be

associated with a year's worth of reproductive effort. Thus, males chosen as extra-pair partners by females enjoy the possibility of a large immediate benefit (paternity of offspring who will be reared by the female with the help of another male) and similarly inflict a large cost on the "cuckolded" or genetically displaced male. These large potential selective effects would explain both a male's eagerness to indulge in such extra-pair copulations and his anxiety that his own mate might act similarly!"

"Bateman '48 in Heredity"

Were it not for Ernst Mayr I would never have heard of "Bateman '48 in Heredity." I was taking a reading course from him on genetics and having done no reading on genetics I told him pigeon stories. "Have you read 'Bateman '48 in Heredity'?" (Never heard of it.) "Go read it; it has the key to what you are talking about."

Three weeks later I returned and still not having done any work on genetics, I launched more pigeon stories at him, when he briskly cut me off: "Have you YET read 'Bateman '48 in Heredity'?' No, I had not. "I will not continue this conversation until you have," Mayr said, turning away from me. That was how Ernst Mayr made sure I read the key paper—*Bateman 1948 in Heredity*!

And read it I did. That evening I xeroxed the paper when Harvard did not charge a graduate student for doing so.

And Bateman *was* the key. It had variance in reproductive success as a function of differences in relative parental investment; the less investment in offspring, the higher variance in their number. The variance data were unambiguous: 4 percent of females had 0 reproductive success; the rest varied by their ability to produce eggs. Fully 21 percent of males had no surviving offspring. This was because of low male parental investment. The cost of sperm was trivial compared to the cost of eggs. So, males were in competition with each other and some did better. They either outmuscled their brothers or they were more attractive to females.

It is interesting that no one, but no one, cited "Bateman '48 in Heredity." The paper was completely overlooked. Ironically, "Bateman '49," a trivial paper on Drosophila genetics, was cited numerous times. For me, "Bateman '48 in Heredity" immediately opened up a brand-new world unexplored by others—the connection between variance in reproductive success and relative parental investment. The latter was defined by the tendency for parental investment to inhibit future parental investment. Eggs vs. sperm. All I had to do was fill in the details.

George Williams had a strong influence on my thinking, of which I became conscious only after I had finished writing the chapter. I was about to teach a course at Harvard in 1971 on natural selection and social behavior in the anthropology department under Irv DeVore. Since I was preparing for the course, I reread Williams (1966) and was astonished to see how much of my own chapter was borrowed from his book. Sex role reversed species. Very simple. Males invest more than females. So, there's a sex role reversal based on sex reversal in parental investment. Differential mortality by sex. Which sex dies faster under what conditions? He did not solve the over-age-17 problem, but he raised it. There were other examples.

Citations

Parental investment and sexual selection has been cited more than 17,000 times. This is extremely high for a theoretical paper, one of the top 5 of 30 million. It is not a direct measure of importance or quality. For example, the most important paper published in all of 20th-century biology was Watson and Crick (1953), which gave the structure of DNA, the double helix. It has been cited *half* as often as reciprocal altruism which has been cited some 13,000 times. Sometimes I like to joke that of course Watson and Crick is less important than reciprocal altruism, but is it really less than *half* as important as reciprocal altruism, as the data would actually suggest?

Why is a paper cited so often? On the one hand, parental investment and sexual selection give you a general theory for the evolution of sex differences in all species. They therefore apply wherever there are two sexes. And they link together data from all different species.

Perhaps more important than a general theory of sex differences, parental investment and sexual selection defined parental investment. And it was different than parental care, it was different than cost of parental care. It was parental investment and an analogy between growth of populations and growth of money. You invest money to get back more money in the future. You invest in current offspring in order to get more offspring in the future. Once you define a variable, it is natural to get cited whenever it is first used.

The Writing of the Chapter

I wrote the chapter in several stages.

I began by rereading the entire literature start to finish. I had assembled about

70 articles over two or three years. Some principles became obvious when the whole literature was read, while only suspected from reading the literature one by one. I was supposed to be focused on amphibians and reptiles and decided to concentrate on differential mortality by sex as the only topic they might contribute to. Alas, data from nature were useless since they measured not adult sex ratio but ease of capture—males disperse more widely, so they encounter traps more frequently and are less timid so they enter them more often.

I therefore expanded my subject to include all organisms.

This stage took about seven months, reading the entire available literature and organizing it into subcategories.

I then decided to embed the entire literature simultaneously in my brain "without fear or favor" (e.g., bias due to time of acquisition). To do so, I mixed all the papers up at random and then spent the next three days speed-reading the whole lot.

At this point I was ready to write the paper. I spent about nine weeks writing the chapter itself. Emended and improved since then, but what you see is what you got.

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CHAPTER
2

Sexual Selection and the Animal's Mating Mind

Michael J. Ryan

Abstract

Moving from Darwin's theory of natural selection, I briefly review his theory of sexual selection and focus on his idea of female mate choice and the sexual aesthetics that motivate it. I review some early hypotheses on the adaptive significance of mate choice. Going forward, I then introduce studies that attempt to uncover the underlying mechanisms that define a female's sexual aesthetics. Much of evolutionary psychology has been derived from basic notions in evolutionary biology, especially in mate choice. Here, I turn the tables and review studies of animal mate preferences that have been inspired by studies of humans in the fields of psychophysics, behavioral economics, and neuroaesthetics.

Key Words: sexual selection, mate choice, psychophysics, sexual beauty, irrational choice

Sexual Selection Theory

It has been 150 years since the publication of *The Descent of Man and Selection in Relation to Sex* (Darwin 1871), and a bit longer since Charles Darwin exclaimed, "… the sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!" (Darwin 1860). Darwin already had one important theory, natural selection, under his belt when he turned his attention to what initially seemed to be a contradictory theory, sexual selection.

Darwin had an aversive reaction to the peacock's tail because the mere existence of this ornament seemed to run counter to predictions of natural

selection, the evolution of traits that enhance survivorship. The peacock's tail is not an isolated example. Elaborate traits that seem to compromise survivorship are found throughout the animal kingdom among most sexually reproducing taxa, and these ornaments are perceived in all sensory modalities. These types of traits include birdsong, cricket and frog calls, firefly flashes, brilliant colors of many fish, and the musty odors of many mammals. These traits share other attributes: they are involved in mating behavior and they are sexually dimorphic, often being more extensively developed in males than in females.

In retrospect, Darwin's sexual selection hypothesis does not seem complex. Like natural selection, evolution by sexual selection requires variation, selection, and inheritance. The difference is in the second step. Natural selection favors those variants with higher survivorship while sexual selection favors those variants with greater mating success. Darwin suggested that sexual selection favored two types of traits: those that enhanced an individual's access to members of the other sex and traits that made courters more attractive to members of the opposite sex, the choosers; in short, armaments and ornaments. An important caveat is that there is substantial variation in the animal kingdom, and there are cases in which females exhibit the more elaborate courtship traits and other species, such as our own, in which males and females both exhibit these types of traits (Rosenthal 2017). Nevertheless, Darwin posited that in most animal mating systems, males are competing for either access to or the attention of females.

Male-male competition was not a controversial idea perhaps for several reasons (Richards 2017; Ryan 2021). Males battling for access to females did not seem all that different from activities favored by natural selection and conformed to Tennyson's epitaph that nature was "red in tooth and claw." The idea of mate choice, however, rankled many of Darwin's supporters, especially Alfred Russel Wallace. Many of Darwin's contemporaries had a hard time empowering female animals as the agents who decide who gets to mate, and they also found Darwin's explanation of why females have these preferences, that they were grounded in the female's sexual aesthetics, as rather wanting. Darwin's theory laid mostly fallow for about a century (Richards 2017; Ryan 2021).

There was a resurgence of interest in sexual selection by mate choice one hundred years later that resulted in large part from Campbell's edited book *Sexual Selection and the Descent of Man, 1871-1971* (Campbell 1972), and especially Trivers's (1972) chapter on parental investment and sexual selection. Trivers was influenced by the early work of Bateman (1948), who showed that in fruit flies the number of matings had a larger effect on male reproductive success than on female reproductive success. Trivers pointed out that this

discrepancy arises from greater female investment in her gametes than male investment in his gametes. This gives rise to a sexual conflict of interest (Arnqvist and Rowe 2005) in which males should be under selection to mate often and females should be under selection to mate carefully. A point sometimes overlooked by critics in the social sciences is that this formulation firmly planted females in the driver's seat; they were the deciders. But when Darwin moved on to discuss humans, he returned to a more Victorian view of the sexes (Richards 2017).

Bateman's principle, as it is now called, has been productively criticized on a number of fronts (Gowaty et al. 2012; Tang-Martínez 2016). A recent meta-analysis of a large number of mating systems, however, upheld Bateman's and Trivers's prediction of these sex differences in mating roles (Janicke et al, 2016). In addition, Borgerhoff Mulder and Ross (2019) critically and carefully applied Bateman's principle to their analyses of twenty years of data on marriage systems of the Pimbwe in East Africa.

Darwin's theory of sexual selection by mate choice has attracted more attention and consternation than his theory about male competition for access to females. It was much easier to explain the evolution of armaments than ornaments. Post-Trivers, behavioral ecologists showed that in many cases female mate choice garnered resources that increased her reproductive success. But the question that seemed to most interest behavioral ecologists was what kind of information about the male's genetic quality is communicated to the choosing females. The good gene's hypothesis posits that males advertise genes that enhance survivorship, and females are under selection to choose these males because of the genetic benefits to their offspring (Hamilton and Zuk 1982; Rowe and Houle 1996; Zahavi 1975). Theory suggests this hypothesis is logical (Grafen 1990), but there is not overwhelming empirical support that it is biological. Surely, good genes selection occurs, but estimates of its relative effect in nature are relatively small (Achorn and Rosenthal 2020; Kirkpatrick and Barton 1997; Møller and Alatalo 1999; Rosenthal 2017).

More recently, research in the realm of sensory ecology, neuroethology, and neuroscience have shown how selection on sensory, neural, and cognitive systems in other domains can have important influences on what females find sexually beautiful. These studies are providing important insights into the scaffolding of an animal's sexual aesthetics. This is the line of research I follow in the remainder of this chapter.

Sexual Selection and Evolutionary Psychology

Evolutionary biologists have long been interested in human biology, and especially human behavior. Darwin is a prime example (Darwin 1871, 1872). Much of the current interest in the evolutionary basis of human behavior probably has its roots in *Sociobiology* (Wilson 1975). That book, and especially the last chapter, "Man: From Sociobiology to Sociology," both garnered the most criticism from the general audience and also provided the foundation for evolutionary psychology. Many of the subjects in evolutionary psychology (e.g., altruism, mutualism, war, and sex) address ideas that populated that chapter (Barkow et al. 1992; Buss 1994; Miller 2011). Thus it seems fair to say that evolutionary biology writ large has inspired much of what is going on today in evolutionary psychology.

I am going to turn the tables. I am going to review a number of recent avenues of interest in animal sexual selection and mate choice that are inspired by studies of humans, especially in the fields of psychophysics, behavioral economics, and neuroaesthetics.

Cognitive Aspects of Mate Choice

A number of researchers working parallel to or collaborating with behavioral ecologists have delved into the neural underpinnings of female preferences. What is it about the female's brain that makes her perceive some traits as more attractive than others? In a variety of taxa and in all sensory modalities, researchers have uncovered neural biases at the sensory periphery and neural circuits in the brain that contribute to the female's sexual aesthetics (e.g., Endler 1992; Gerhardt and Huber 2002; Greenfield 2002; Wilczynski and Ryan 2010).

Although these studies in neuroscience have provided unparalleled understanding of the neural scaffolding of the female's sexual aesthetics, another set of questions concerns the cognitive aspects of mating decisions. By the animal's cognitive processes we refer to Shettleworth (1998), who defines cognition as the acquisition and analysis of information in the environment that contributes to decision-making. I will review a number of studies, including several that we conducted with túngara frogs, that were inspired by studies of human behavior.

Weber's Law

We know from the notion of the *Umwelt* by von Uexküll (1982; see also Caves et al. 2019) that different animals perceive the environment in different ways. This is obvious when we compare the sensory limitations of ourselves to

other animals. For example, we cannot hear the ultrasonic echolocation calls of bats nor the infrasound of elephants; we cannot see in the ultraviolet as can bees, fish, and birds, nor can we sense infrared with the precision of a rattlesnake. We cannot share the olfactory experiences of man's best friend and are unable to sense the signals of most electric fish.

Another limitation is how we compare stimuli within a range we can sense. Psychophysics is a field with a long and distinguished history that is concerned with how we translate stimuli into perception. Many studies show that humans, and other animals as well, do not compare stimulus intensities as they actually exist; our perceived difference between stimuli is often not based on absolute (linear) differences but on proportional ones. These studies are often done in the context of just noticeable differences (JNDs): the minimum difference between two stimuli for us to perceive them as different. Akre and Johnsen (2014) reviewed a number of studies in humans (as well as other animals) showing proportional comparisons in different sensory modalities: in hearing in terms of amplitude and frequency comparisons; in vision in terms of comparisons of area, intensity, and wavelength; in temporal duration in both auditory and visual domains; and in our number sense (see also Shepard 1987).

Although there are exceptions, many of these comparisons follows Weber's law, which is $\Delta I = kI$, where ΔI is the JND, the magnitude of the stimulus is I and k is a constant. What is clear from this equation is that as stimuli become larger in magnitude, their differences must be greater for us to be able to detect differences between them. In the context of animal behavior in the wild, we are more concerned with just meaningful difference (JMDs; Nelson and Marler 1990) than JNDs.

Mate choice is all about comparisons whether it is between two or more individuals or one individual and a neural template; it is of some importance that we understand how these comparisons are made. In 1984, Cohen (1984) asked if these female comparisons followed Weber's law; it took more than twenty-five years to get an answer.

Túngara frogs have become a useful system for asking questions about sexual selection and communication. As I refer to this system several times, it is worthwhile to summarize the mating system (Ryan 1985, 2011). These frogs breed during the rainy season in much of the New World Tropics. Males gather in choruses and call for females. Females choose the males with whom they want to mate, the male and the female construct a foam nest with about two hundred fifty eggs that hatch within a few days. There is no parental care of the eggs once the nest is constructed. As with most frogs, the female's mate choice is based primarily on the male's call. The call contains two components, a whine

which may or may not be followed by chucks. The whine is necessary and sufficient to attract females for mating, but the addition of even a single chuck, they can add up to seven, increases a male's attractiveness to the female fivefold. Females also tend to prefer more chucks to fewer chucks. Despite the sexual potency of chucks, males only add chucks when vocally competing with other males, even though all males are capable of producing chucks. The benefit of adding chucks is countered by the frog-eating bat. They are attracted to the male's mating call and like the female frogs are about five times more attracted to calls with chucks than calls without chucks; the difference being that females are searching for a mate while the bats are searching for a meal.

Females prefer more chucks to fewer chucks, but how is that comparison made, are they comparing absolute numbers of chucks or is the comparison proportional? If they are following Weber's law, we would predict, for example, that the strength of preference for six chucks versus five chucks would be less than the strength of preference for two chucks versus one chuck. If, on the other hand, they are comparing absolute chuck number, then the strength of preference should be the same. Akre et al. (2011) tested female frogs in two-choice phonotaxis tests in which the two stimuli had the same whine but varied in the number of chucks. The strength of preference was estimated by the proportion of females that preferred the call with more chucks. Proportional differences in the number of chucks explained significantly more of the variation in the strength of preference than did the absolute differences in the numbers of chucks (84 percent vs. 12 percent; fig. 2.1).

Are proportional comparisons an adaptive strategy for mate choice in túngara frogs, or is this just the way that many brains make comparisons? If the latter is the case, we might expect frog-eating bats to also follow a Weber-like function when comparing chuck number. Analogous choice experiments conducted with the bats with the same call stimuli revealed strikingly similar results: proportional differences in the number of chucks explained 74 percent of the variation in the strength of preference while absolute differences in chuck number explained only 8 percent of the variation in the strength of preference (fig. 2.1). These results can have important consequences for how sexual selection proceeds. They suggest that as a sexual trait increases in magnitude, a peacock's tail for instance, a male must be absolutely more and more different than his competitors to be perceived as more attractive. We know that natural selection is an important counterselection force on the evolution of elaborate male courtship traits (Kirkpatrick and Ryan 1991), but this study suggests there is also a cognitive brake on the evolution of exaggeration.

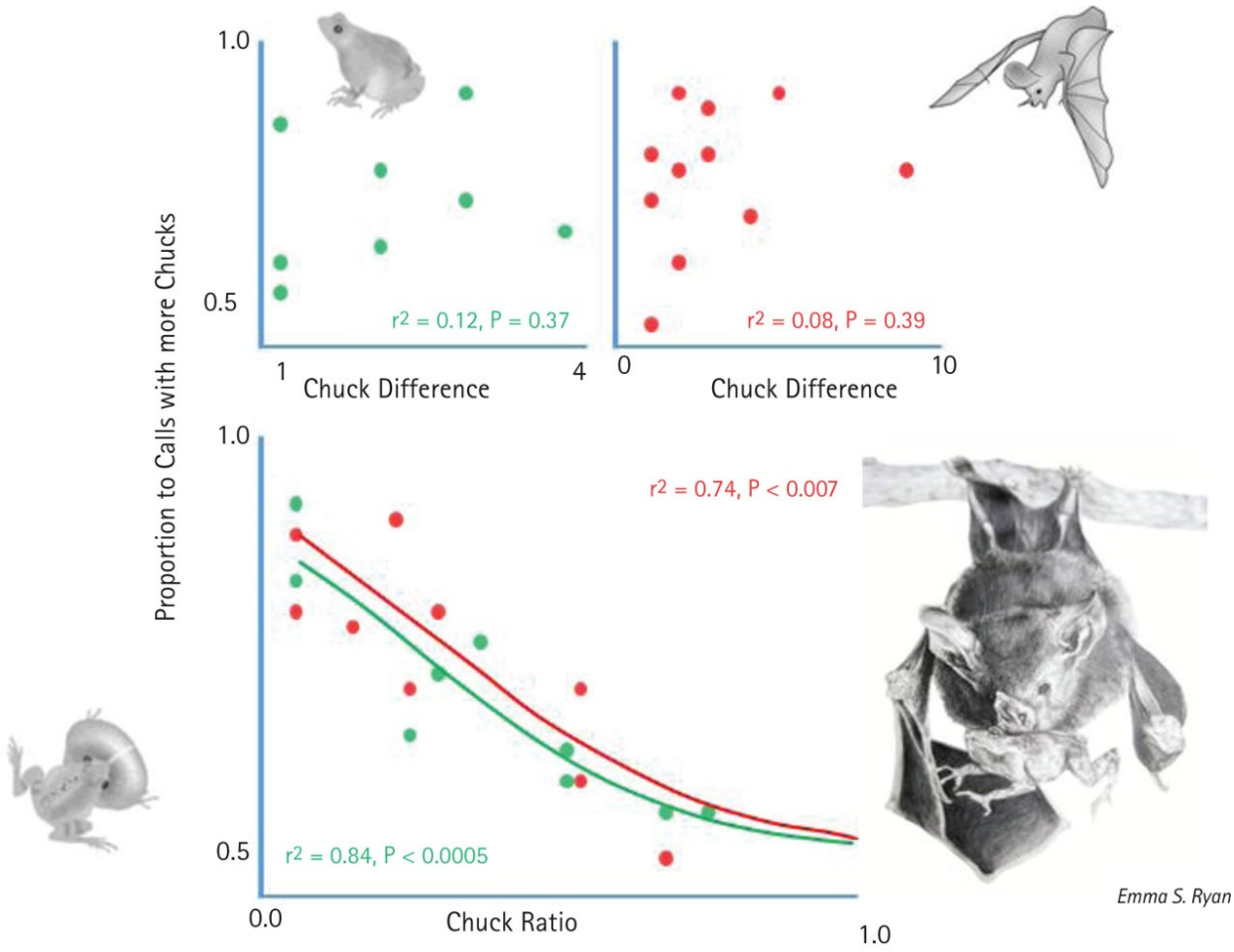

Figure 2.1 The proportion of female túngara frogs (green) and frog-eating bats (red) that preferred the call with more chucks as a function of the difference in the number of chucks being broadcast from each speaker (top) or the ratio of chuck number being broadcast from each speaker (bottom).

Although it has long been known that humans often follow Weber's law when comparing stimulus magnitude (see above), Gassen et al. (2022) recently showed proportional comparisons when humans compare facial attractiveness. They used morphing software to generate faces that varied between photos that were prerated as below and above average in attractiveness. The results revealed that the judges were making proportional comparisons, images for the more attractive faces had to be more different quantitatively to be perceived as more attractive. These results were also consistent with simultaneous eye-tracking data.

Spatial Illusions

Holding distance constant, we see larger objects as larger than smaller ones because they subtend a greater angle of the retina. Holding size constant, we

perceive closer objects as closer for the same reason. But we are usually able to parse the effects of size and distance due to what has been called size–distance invariance. Although vision researchers still do not understand exactly how this happens, we know that the invariance phenomenon is not all that invariant (Kim et al. 2016). But we also know that we don't get fooled into thinking that the coffee cup in front of us is larger than a more distant building. Filmmakers, photographers, and architects have been able to exploit this size–distance phenomenon in a myriad of applications.

When we view a building with several floors we implicitly assume that the exterior windows are all the same size even though the windows on higher floors appear smaller. The perceived size difference between the windows on the ground floor and the top floor gives us an estimate of the height of the building. Cinderella's Castle at Walt Disney's Magic Kingdom creates a perceptual illusion by toying with our size–distance relationships. The castle windows in the upper floors are absolutely smaller than the windows on the ground floor. We do not know that when we look at the castle, and thus the castle appears taller to us than it actually is (Ryan 2018).

We know that animals have evolved a variety of patterns to manipulate the perceptions of their predators to afford themselves a modicum of safety (Stevens and Merilaita 2009). Greater Bower birds exploit perceptual biases in the mating domain. Males construct a bower; its function is to provide an arena in which males display to females standing in an avenue that leads up to the bower. The males decorate the avenue with a variety of objects, such as stones and shells. But they do not do so in a haphazard manner. The larger objects are placed closer to the bower and the smaller objects farther away. This creates a forced perspective the opposite of the Cinderella Castle, the bower appears smaller than it actually is. Endler and his colleagues suggested that the male courting in the bower now appears larger and thus more attractive to the female (Endler et al. 2010). Data on male mating success collected in the wild supports their hypothesis (Kelley and Endler 2012).

Auditory Illusions

Studies of two auditory illusions have inspired some studies of mate choice in túngara frogs. The first is the McGurk effect, which is described as "hearing lips and seeing voices" (McGurk and MacDonald 1976). In these experiments, the sound of a phoneme is morphed onto a video of lips speaking a different phoneme. Amazingly, the observer perceives a third phoneme. For example, the sound of /ba-ba/ is morphed onto the video of lips speaking /ga-ga/; instead of

perceiving either of these two phonemes, the observer instead perceives /da-da/. These studies show that auditory and visual stimuli, and probably other multimodal stimuli, are not perceived as individual elements but as an integrated whole.

Another auditory illusion is referred to as auditory continuity (Bregman 1994). Researchers present the observer a pure tone with a silent gap in the middle. Observers clearly perceive the two separate segments of the tone. They then added white noise to the gap and increased the amplitude of the white noise until the observer hears a continuous tone. This study shows how auditory perception can fill in gaps with meaningful stimuli, much as our visual system fills in blind spots (Pessoa et al. 1998).

Like most frogs, túngara frogs have vocal sacs that inflate and deflate synchronously with the call. The vocal sac increases the visual conspicuousness of the calling male and it also influences the female's mate choice. She is more attracted to a standard call (e.g., a whine-chuck) that is paired with an inflating vocal sac of a robo-frog compared to the same call by itself (Taylor and Ryan 2013; fig. 2.2). As with the McGurk effect, the temporal relationship between the call and the vocal sac influences the female's perception. If the vocal sac is inflated after the call, then the visual cue does not enhance the call's attractiveness; in fact, it makes it less attractive (fig. 2.2). Temporal relationships of the acoustic call components also influence the saliency of the acoustic signal. In a normal call, the chuck immediately follows the whine, which is about 300 ms from the beginning of the whine. If the chuck is displaced so that it is now 500 ms from the initiation of the whine, the chuck no longer increases the attractiveness of the whine (fig. 2.2). If these two unattractive signals are combined, a whine followed immediately by the vocal sac inflation and the 500 ms-displaced chuck, this unnatural multimodal signal is as attractive as a standard whine chuck (fig. 2.2). The interpretation is that the presence of the vocal sac perceptually rescues the displaced chuck; that is, it creates a multisensory illusion in the female so that she now perceptually binds these three components into a single perceptual unit (Taylor and Ryan 2013). This is especially interesting because these frogs did not exhibit auditory continuity in manipulations of the whine (Baugh et al. 2016) or when white noise was produced between the whine and the temporally displaced chuck (R. Taylor, unpublished data).

Mate Choice Copying

Before mate choice copying was a thing, psychologists had shown that social

perceptions of a man could be influenced by the attractiveness of a female consort. The experiment was quite simple (Sigall and Landy 1973). A subject entered a waiting room where there was already one man and one woman. The man was of average attractiveness and the woman was judged as either attractive or unattractive. The subject was asked to rate the degree to which they might like or dislike the man; the subjects rated the man with the more attractive woman as more likable. Even though this study was not specifically addressing sexual attractiveness, it clearly shows that the halo cast by the woman was dependent on her attractiveness. Numerous other studies have shown similar effects in humans in the context of mate choice copying (Hill and Buss 2008).

Studies of mate choice copying in animals became a widely studied phenomenon after Dugatkin's pioneering studies of guppies. Guppies are quite variably colored fish and a number of studies have shown that females prefer males with more orange (Houde 1997). Dugatkin (1992) conducted a simple experiment that quickly became a standard for animal mate choice studies. A focal female was placed in an aquarium in which there was a male on each side separated from the focal female by a pane of glass. The female could freely move within the aquarium and be courted by each male on the other side of the glass divider. As had been shown in previous experiments, the focal female spent more time courting the male with more orange. The focal female was then moved back to the middle of the aquarium and constrained inside a glass cylinder. A live "model" female guppy was placed with the less preferred male and the focal female could observe the two interacting. The model female was removed, the choice test was repeated, and the focal female now switched her preference to the previously less preferred male. The interpretation was that the perceived attractiveness of the male increased once he was observed courting another female.

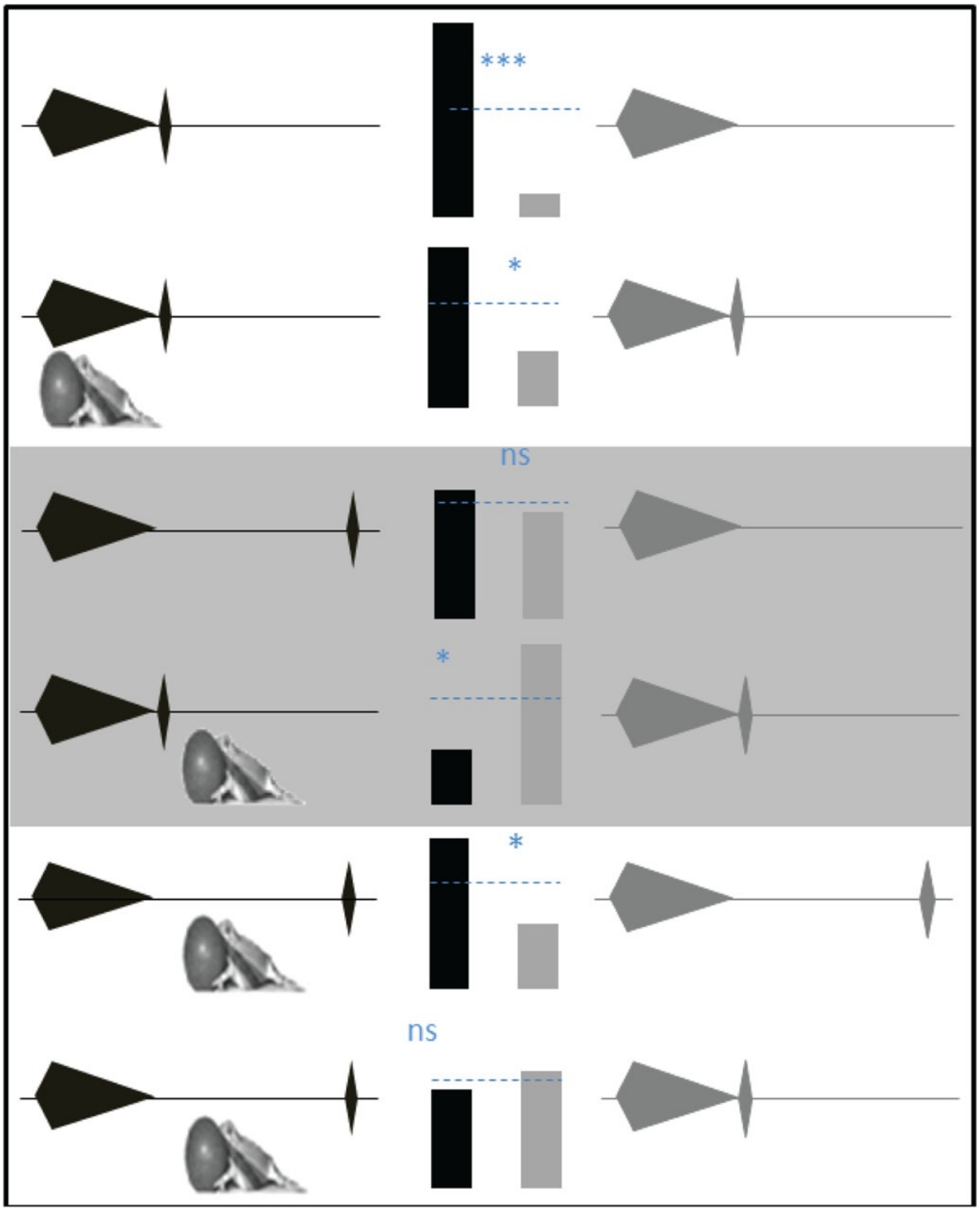

Figure 2.2 Results of phonotaxis experiments between the stimulus on the left (black) and the stimulus on the right (gray). Black bars represent the proportion of responses to the black stimulus, gray bars represent the proportion of responses to the gray stimulus. The image of the robo-frog indicates the presence and temporal occurrence of the visual stimulus, an inflating–deflating vocal sac. In the top panel: females prefer

a whine-chuck to a whine, and they prefer a whine-chuck associated with an inflating vocal sac versus a whine-chuck with no visual stimulus. In the middle panel: females did not discriminate between a whine with a silent gap followed by a chuck versus a whine only, while the females preferred a whine-chuck to a whine-chuck associated with the visual stimulus when vocal sac inflation occurred at the end rather than at the beginning of the call. In the bottom panel: females preferred a whine followed by an inflating vocal sac followed by a chuck compared to the same call without the visual stimulus; the whine–vocal sac inflation–chuck was as attractive as a normal whine-chuck. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

A mate choice copying study helped resolve a conundrum in another species of fish. The sailfin molly is found from coastal central Mexico around the Gulf of Mexico and up the eastern seaboard of the United States to the Carolinas. Like most fish, they reproduce sexually. The Amazon molly, however, is an all-female species that reproduces clonally; however, females must acquire sperm to trigger development of their clonal eggs, there is no fertilization. One of the species they mate with is the sailfin molly. The association between the sexual and asexual species raises a number of questions, one of which is—why would a male sailfin molly mate with an Amazon molly since the mating will not contribute to his reproductive success? It was thought that males might not be able to discriminate between their own females and Amazon females, but that is not true. Even in areas where Amazons do not occur, male sailfins prefer females of their own species over Amazon females (Gabor and Ryan 2001; Ryan et al. 1996). A mate choice copying experiment similar to the one conducted with guppies by Dugatkin suggested an answer. A focal sailfin female was given a choice between two male sailfins and predictably she preferred the larger male. In this experiment, a model Amazon female was added to each of the chambers with a male, but the focal sailfin female could only see the less preferred male interacting with the Amazon, her vision of the model Amazon with the preferred male was blocked so she could only see the male. The choice experiment was repeated and, as with the guppies, the female sailfin spent significantly more time with the smaller male whom she had just observed courting an Amazon (Schlup et al. 1994). The same experiment was later replicated in the field (Witte and Ryan 2002). The interpretation is that even though males do not accrue an immediate reproductive benefit by mating with Amazons, their attractiveness in the eyes of their own females, and supposedly their future reproductive success increases.

Hill and Ryan (2006) then asked if the attractiveness of the model influences the degree of mate copying, much as the attractiveness of a female consort influenced the likability of her male associate in the human study discussed above. Also as noted above, male sailfins can discriminate between female sailfins and Amazons and prefer to court their own species. In the eyes of males,

female sailfins are higher-quality mates than Amazons. Female sailfins can also discriminate between female sailfins and Amazons.

The researchers conducted similar mate copying studies just described but with a twist. After the initial choice the less preferred male was paired with a female sailfin while the preferred male was paired with an Amazon female. The focal female was able to observe each of these males courting his model female, the model females were then removed and the choice test repeated. Focal females significantly increased their time associating with the previously unpreferred male who had just been courting a high-quality female and decreased the amount of time spent courting the previously preferred male who had just been observed courting a lesser-quality female. Thus, not only does the presence of the female influence a male's attractiveness, but the female's attractiveness itself influences the male's attractiveness.

Mate choice copying has been demonstrated in numerous animals, not just in fish, and there have been a number of suggestions as to why it is adaptive for females to exhibit mate choice copying. Less attention has been given to the hypothesis that mate choice copying is just one manifestation of a more domain-general type of social facilitation (Westneat et al. 2000). As I argued that following a Weber-like function in comparing mates is not an adaptation for mate choice per se in túngara frogs, the same might be true in mate choice copying. There is some evidence for this idea in humans. Heterosexual women viewed photographs of men's faces on a computer screen, received feedback in real time as to the ratings given by other subjects, and were then able to change their rating. The results showed that subjects changed their rating of facial attractiveness in response to feedback from others. For every 1.0 point difference from the feedback score, the subject changed her rating by 0.13 points. The magnitude of this effect, however, was similar in an analogous experiment that rated the attractiveness of hands, a change of 0.13, and abstract art, a change of 0.14. Their conclusion was that mate choice copying in humans might be one expression of a broader domain-general social facilitation and not necessarily an adaptation for mate choice per se (Street et al. 2018).

Closing Time

In 1979, Pennebaker et al. (1979) published an interesting paper under the title *Don't the Girls' Get Prettier at Closing Time: A Country and Western Application to Psychology*. This study was inspired by the lyrics of the song by Mickey Gilley, which suggested the perceived attractiveness of other-sex patrons in a bar increases as closing time approaches. Their data supported Gilley's

narrative. For both men and women, the attractiveness of opposite-sex but not same-sex individuals increased as closing time neared.

One possible explanation of these results is state-dependent valuation. For example, individuals place greater value on food items they consumed when they were hungry versus food items they consumed while they were satiated (Hemingway et al. 2020; Pompilio et al. 2006). Pennebaker et al. offered another explanation based on the psychological theory of dissonance: “If the subject were committed to going home with the person of the opposite sex, it would be dissonant to consider an unattractive partner. The most efficient way of reducing such dissonance could be to increase the perceived attractiveness of the prospective alternatives.” If so, the next morning the judging person would not experience cognitive dissonance along with his hangover.

Alcohol was one key variable that was not controlled in the closing time study. The beer goggles effect is well known and a number of studies have documented how blood alcohol content (BAC) by itself influences perceptions of attractiveness (Lyvers et al. 2011). The Pennebaker study was replicated in Australia in which closing time as well as BAC was measured (Johnco et al. 2010). Both of these factors contributed independently to the closing time effect. The closing time effect generated a number of other studies of humans, but it also inspired one of our studies of túngara frogs.

Although male túngara frogs spend many nights at the chorus advertising for females, females only attend the chorus on the night they mate. If they do not mate by the end of the night they drop their eggs without being fertilized. It takes the female another six weeks to yoke up another set of eggs, a substantial time given that the breeding season is only about six months long and males and females both seem to live less than a year. Lynch et al. (2005) conducted a repeated-measures test in which females were tested early in the evening and then late in the evening, about the time they would normally drop their eggs if not mated. The females were tested with a synthetic call that was a “hybrid” between the call of the túngara frog and another species. Females were tested in one-choice tests to determine if the signal was attractive enough to elicit female phonotaxis. Early in the evening, only 29 percent of the females were attracted to this call. Later in the evening more than half of the females, 53 percent, found this call sufficiently attractive. Not only was there a significant closing time effect on call acceptance, the latency to respond to the signal was significantly faster later in the night, 404 versus 617 seconds.

Closing time can occur in different contexts. In Pennebaker’s study and the frog study, closing time referred to the nightly end of the sexual marketplace. Another “closing time” that occurs in humans is the phase of ovulation. Haselton

and her colleagues tested their "fertility ornamentation" hypothesis by examining how women dress during the fertile and nonfertile periods of their menstrual cycle (Haselton et al. 2007). Women were photographed during each stage and the photographs were shown to judges. In accord with the researchers' predictions, women were judged as being more attractive during the ovulatory phase than the nonovulatory phase, the effect being due to the women's dress. In another study, Haselton showed that females spoke in higher-pitched more feminine voices during the fertile period (Bryant and Haselton 2009).

A biological clock in women at a much larger scale marks the countdown toward menopause, at which time reproduction is no longer an option. Easton and her colleagues propose that women have a "reproduction expediting psychological adaptation" (Easton et al. 2010: 516). In translation, this predicts that women should be more interested in sex when they are older. The research supports this hypothesis as middle-aged women not only fantasize about sex more than younger women but actually have more sex.

Male fruit flies also exhibit greater interest in sex when they are older, and at the mechanistic level we know why. Males have mature sperm two days after they emerge from their pupal case. But these males are less fertile than males that are seven days old. For both females and males, mating shortens their life, so it was predicted that males should delay mating with females until they are older and more sexually mature. This is what the researchers found (Lone et al. 2015). What is modulating this difference in sexual motivation? Males detect female pheromones with olfactory receptor neurons. When the researchers recorded neural responses to female pheromones in these olfactory receptors they showed that the neurons were one hundred times more sensitive in seven-day-old males than in two-day-old males, explaining at a mechanistic level why males were more ready to mate at an older age.

Perceptual Fluency

The field of neuroaesthetics strives to understand the cognitive and neural mechanisms underlying our appreciation for things beautiful. An intriguing idea, which has had its influence on at least one study of animal mate choice, is that of perceptual fluency. This idea was suggested by Reber et al. (2004, 364), who stated that "the more fluently perceivers can process an object, the more positive their aesthetic response." One type of fluency includes sparse coding. This is when an object is encoded in the brain by the firing of relatively few neurons, such as a feature detectors or grandmother cells. This is in contrast to dense coding when a large number of neurons are used to encode a stimulus.

Some support for this study was suggested by Renoult et al. (2016) who trained neural networks modeled after the human primary visual cortex to recognize natural scenes. These models were then presented with women's faces and the amount of neural activity was estimated. Men were then shown the same photographs of women's faces and asked to score attractiveness. The degree of sparse coding explained a significant amount, 17 percent, of the variation in ratings of the women's facial attractiveness. Our visual cortex is important in appreciating visual beauty, but it surely did not evolve to encode facial attractiveness. The researchers suggest that the details of visual encoding probably evolved under selection to extract information about the visual world around us. This somewhat parallels finding by Changizi et al. (2006) who proposed a similar hypothesis to explain the evolution of forms used in written alphabets. There was a strong correlation between the forms of letters and the patterns in natural visual scenes.

How might this apply to animal mate choice? Renoult, Mendelson, and others (Renoult and Mendelson 2019) suggested that the hedonic value of perceptual fluency might underlie the motivation of females to seek out males with certain visual courtship patterns. This was tested by Mendelson and her colleagues (Hulse et al. 2020) with darters. These freshwater fish have a variety of habitats, and males exhibit conspicuous patterning during the breeding season. The researchers characterized the spatial statistics of the habitat and male and female color patterns using spatial Fourier analysis. For each measure, they plotted power over frequency and used the slope of that relationship to describe the pattern. The researchers showed that the pattern of the males' courtship coloration significantly matched the local habitats; females showed no such congruence with habitat, and thus it seems unlikely that camouflage is what drove this pattern in the males.

These studies of perceptual fluency are important contributions to sexual selection. If females gain hedonic value from interacting with certain traits this goes a long way in supporting Darwin's notion of sexual aesthetics.

Summary

Cognitive psychology and cognitive neuroscience have made great strides in understanding how human and human-model systems analyze information to make informed decisions. These fields have already had an important influence on animal foraging behavior (Kacelnik 2006), but less so on animal mate choice.

With the resurrection of interest in sexual selection in the 1970–1980s, studies of animal mate choice mostly focused on signal content of male

courtship displays and the adaptive significance of female mate choice. Eventually, interest turned toward integrating evolutionary and mechanistic studies to get a deeper understanding of animal sexual aesthetics. Most recently, a number of researchers have been addressing issues related to the role of cognition in mate choice, and as I have shown here, many of these studies are inspired by research typically conducted in humans. I suggest that studies in cognitive psychology and cognitive neuroscience contain a trove of potential insights into how animals make mate choice decisions. Such integration and interaction will not only give insights about mate choice but allow us, at a more global scale, to evaluate the degree of continuity or noncontinuity between the mind of the animal and the mind of the human (Cheney and Seyfarth 2008; Griffin 2013).

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CHAPTER
3

The Interface of Sexual Selection, Conflict, and Evolutionary Psychology: Emerging Core Themes

Jennifer C. Perry and Tracey Chapman

Abstract

Evolutionary perspectives from sexual selection and sexual conflict can give powerful insight into the ultimate reasons for the existence of seemingly paradoxical traits such as exaggerated sexual characteristics and sexual exploitation. However, our biological and psychological understanding of such traits is often hampered by a lack of integration across different taxon-focused research fields, as well as by perceived difficulties of integrating human culture into standard evolutionary paradigms. Our aim is address these limitations and to identify emergent, general themes by discussing sexual selection and sexual conflict at the interface of evolutionary biology and evolutionary psychology. We focus mainly on the theme of sexual conflict, which occurs when males and females maximize their evolutionary fitness in different ways. We begin by reviewing core concepts and key examples from diverse species. We then explore whether these ideas can usefully be applied to the study of reproductive interactions in humans. This exercise shows that even theory drawn from the study of animal biology, which focuses only on the evolutionary consequences of sexual interactions, has surprising power to explain diverse facets of human mating behavior.

Key Words: sexually antagonistic coevolution, fitness, social behavior, sexual selection, sexual environment, mate choice

Sexual Selection and Sexual Conflict—The Fundamentals

Sexual selection focuses on traits that serve to ensure success in reproduction (Darwin 1871). Two major forms are usually identified: that which occurs within sexes and the choice that occurs between them. Sexual selection can shape the evolution of traits related to courtship and the acquisition of matings through to interactions that occur after mating itself. In-depth reviews of the exuberant wealth of adaptations that are shaped by sexual selection have been made elsewhere (Andersson 1994). However, sexual selection does not simply describe the adaptation of bright colors, showy tails, and choosiness. Because measures of "quality" (referring to the most competitive and successful individuals or those chosen as mates) can capture the influence of many loci across genomes, the success or choice of quality individuals has genome-wide consequences. Therefore, sexual selection can purge deleterious mutations and influence the probability of speciation and extinction (Hollis et al. 2008; Lumley et al. 2015; Ritchie 2007; Whitlock 2000; Whitlock and Agrawal, 2009).

In this chapter, we focus mainly on the facet of sexual selection whose existence and importance started to emerge in the 1970s: namely, sexual conflict. This recognition was driven by observations of the preponderance of conflictual as well as cooperative interactions between the sexes (Parker, 1979). Since then, the study of sexual conflict has expanded greatly. Its governing influence over diverse and intriguing aspects of reproductive activity and its ultimate consequences for fueling evolutionary change are increasingly realized (Arnqvist and Rowe 2005; Lessells 1999, 2006; Parker 1979; Parker and Partridge 1998).

Sexual Conflict—What Is It and Why Do We Care?

The potential for evolutionary conflict is inevitable whenever the long-term interests of two or more interacting "parties" are imperfectly aligned (Alonzo and Warner 2000; Kokko and Rankin 2006; Mokkonen et al. 2011; Parker 1979; Rowe and Day 2006; Rowe et al. 2005). In these situations, even despite a degree of co-dependency, one party can potentially gain (i.e., transmit their genetic legacy more successfully) even if the other loses (Parker 1979). To be clear, conflicts occur because of differences in the evolutionary interests of genes, but they can be manifested and measured at different levels. For instance, evolutionary conflicts can be observed between genes residing in the nucleus versus those in the mitochondria; genes in a cancer versus in their host; and sex chromosomes with different patterns of inheritance through the sexes, between males versus females, parents versus offspring, and symbionts versus hosts.

What all these conflicts have in common is that the participants do not share each other's vision for the future in terms of how to maximize their fitness (i.e., their genetic representation in subsequent generations). However, rather than being seen as some kind of pathology or process breakdown, these types of evolutionary conflicts should be viewed as expected outcomes of evolution by natural selection. In this they represent a major engine for creating and maintaining genetic variation that provides the fuel for driving, often quite rapid, evolutionary change (Arnqvist and Rowe 2005).

We focus here on the sexual conflicts that occur between males and females. Defined as "a conflict between the evolutionary interests of the two sexes" (Parker 1979) or "sexually antagonistic selection on shared traits" (Rowe and Day 2006), it is increasingly realized that the conditions that can promote the expression of sexual conflict (table 3.1) are very common. There are many reproductive traits over which the sexes may "disagree." The root cause stems from the initial difference between the sexes—their divergent gametic investment in eggs versus sperm (Trivers 1972). This fundamental difference sets in motion potential conflicts over many of the key life history traits. For example, females generally make a larger energetic investment in each gamete (their eggs) and are capable of producing far fewer offspring overall than are males (Bateman 1948; Cluttonbrock and Parker 1992; Emlen and Oring 1977; but see Borgerhoff-Mulder and Ross 2019; Brown et al. 2009b). In many organisms, females also invest heavily in the production and care of offspring. For example, in mammals, females gestate and invest in their young via lactation. In those species that exhibit parental care, females are generally fairly sure of their maternity in the offspring for which they are providing parental care (with exceptions occurring in brood parasites such as the cuckoos and cowbirds; Davies 2010). The set of phenotypes that can successfully achieve this strategy generally require considerable investment in the reproductive processes activated in each reproductive episode, potentially limiting future similar investments. In addition, reproductive decisions that maximize fitness will likely be to limit breeding episodes to those that can be of high quality and maximize the success of those events.

Table 3.1 Factors That Could Affect the Intensity of Sexual Conflict in Mammalian Systems, including in Humans

Factor*	Description	References
Inbreeding—relatedness	Sexual conflict is exacerbated when there is low relatedness between reproducing partners. Low relatedness makes it less likely that currently paired males and females will have a shared evolutionary interest in each other's future.	Bourke, 2009; Dawkins, 1976; Faria et al. 2020; Haig & Wilczek, 2006; Parker,

		1979, 2006; Rankin, 2011
Reproductive context: degree of multiple mating inside and outside a "pair bond" Polygyny (hareem) or polyandry	Here a pair bond refers to the individuals reproducing together in any single reproductive episode. Sexual conflict is exacerbated in nonmonogamous mating systems, as these promote divergence in the genetic interests of males and females in current versus future offspring. If there is a significant chance of additional reproduction with other partners, then sexual conflict will be increased.	Clutton-Brock & Isvaran, 2007; Dawkins, 1976; Parker, 1979, 2006; Rankin, 2011
Paternity assurance	The degree to which a male is sure that the female with which he has recently mated will produce offspring fertilized by his sperm, will influence the extent of conflict. This phenomenon is thought to influence selection for concealed ovulation phenotypes.	Gangestad & Thornhill 2008, Mulder & Rauch 2009
Parental care	Whether one of both sexes provide care and the extent to which they do so can exacerbate sexual conflict (e.g. if one sex can influence the other to provide more care and thus provide less (or none) themselves.	Barta et al. 2002b; Cluttonbrock & Parker, 1992; Liker & Szekely, 2005, Szekely et al. 2007
Reproductive constraint	If individuals Difficult to detect patterns of elevated reproduction in populations reproducing at either a low level or at their upper limit	VanderLaan et al. 2012
Condition	The extent to which individuals can express their genotype, can magnify the differences in quality between individuals and affect the extent to which they can respond to stimuli. Therefore, condition is likely to alter the intensity of sexual conflict. Variation in condition can alter the extent to which males can express potential sexual conflict adaptations and the degree of female responses to them	Amitin & Pitnick, 2007; Fricke et al. 2008, Fricke et al. 2009a, Fricke et al. 2010; McGraw et al. 2007; Rostant et al. 2020; Rowe & Houle, 1996; Rowe et al. 1996
Reproductive physiology	Placental mammals have a strong arena for conflict centered around mothers in the intimate interface between mother and fetus due to placentation and lactation.	Aloise King et al. 2013; Haig, 2004, 2010
Number of mechanisms available	The potential for conflict, may not be manifested if there are limited mechanisms by which each sex can influence the behavior–investment or physiology of the other. This can arise if one sex "wins" a conflict and shuts down the opportunities for the other to influence sexual conflict phenotypes.	Chapman, 2006; Ratnieks et al. 2006
Culture		Buss, 1989, 2013

* These factors feed into the strength of selection for adaptations arising from sexual conflict.

In contrast, males mostly invest much less in the production of each gamete (though it should be noted that ejaculate production as a whole can require considerable investment; Dewsbury 1982; Linklater et al. 2007; Perry and Tse 2013)). Their reproductive potential is generally significantly higher than for

females (Bateman 1948). Males may often also provide less investment in the production of offspring (even in species in which both species provide parental care). Males may generally be less sure of the paternity of offspring for which they are caring. A male's reproductive investment is generally focused on attracting, courting, and securing matings and paternity. Success in these respects may require a very different set of strategies to the optimal female phenotype discussed earlier. In addition, males may gain from reproductive decisions that maximize the number of matings and ensure paternity. These may trade off against the amount of investment given to the female or offspring in any one breeding episode.

These basic differences in the sexes, and the finding that aspects of reproduction are differentially costly for each sex, have been known for many decades (Andersson 1994; Bell and Koufopanou 1986; Partridge and Hurst 1998). The evolutionary tension between the fitness interests of the different sexes outlined above can select for strategies in which one sex (usually males) can gain increased fitness if they can influence or manipulate the way their partner behaves or invests in offspring production, despite any associated costs this may incur (Chapman 2006; Chapman et al. 2003; Holland and Rice 1998, 1999; Krebs and Davies 1987; Parker 1979; Rice 1992, 1996, 1998; Rice and Holland 1997, 1999; Rice et al. 2006). This in turn may select for the manipulated sex to evolve resistance to the manipulation (Chapman 2006; Chapman et al. 2003; Holland and Rice 1998, 1999; Parker 1979; Rice 1992, 1996, 1998; Rice and Holland 1997; Rice et al. 2006).

There can be disagreements between the sexes about most of the major life history traits: for example, the optimum age of sexual maturity, investment in germ line versus soma, who to mate with, how often, how many offspring to have, which sex of offspring to produce, how much to invest in each reproductive episode versus any future offspring, and how much parental care to give (Barta et al. 2002a; Boyko and Marshall 2009; Dawkins and Carlisle 1976; Smuts and Smuts 1993; Stutt and Siva-Jothy 2001; Trivers 1972). These fundamental disagreements can set up a primary battleground between males and females from which an evolutionary response followed by a counterresponse can ensue (Arnqvist and Rowe 2005; Holland and Rice 1998). This process can act as an important driver for generating evolutionary change and maintaining genetic variation (Arnqvist and Rowe 2002a; Chippindale et al. 2001; Fiumera et al. 2006; Rice 1992, 2000).

Broadly speaking, mechanistic approaches to the study of sexual conflict (i.e., those that yield an understanding of how causative traits, underlying genes, or molecular pathways can influence the expression of sexual conflict) can give

valuable insights. Understanding mechanisms can be important because features such as the means by which females respond to males (e.g., quantitatively or as a function of a threshold) can affect whether the outcome of sexual conflict is likely to lead to escalation, or instead, female insensitivity to the male trait (Rowe et al. 2005). Mechanistic information not only provides greater detail about the specific system under study but can also reveal key details of the selective forces likely to be involved.

Ultimately, we are interested in sexual conflict because it can generate and maintain genetic variation to provide the fuel for evolutionary change. Through its effects on the rapid evolution of reproductive traits, it can lead to reproductive divergence and ultimately even speciation (Arnqvist et al. 2000; Gavrilets and Hayashi 2005; Hayashi et al. 2007; Parker and Partridge 1998). Thus, sexual conflict can act as a potent fuel for driving a diverse array of genomic, physiological, morphological, and behavioral adaptations across taxa, as described in more detail later.

Sexual Conflict—Within and between Loci

Sexual conflict has traditionally been explained in terms of conflicts of interest that occur between the same (intralocus) or different (interlocus) genes in males and females (Rice 1998; but see Gardner and Úbeda 2017; Schenkel et al. 2018)). Examples of each proposed route for conflict and the potential mechanisms for their resolution are described in more detail below.

SEXUAL CONFLICT WITHIN LOCI

Intralocus sexual conflict is proposed to occur if there are sex-specific optima for a single trait controlled by the expression of a single gene in both sexes (Bonduriansky and Chenoweth 2009; Chippindale et al. 2001; Fedorka and Mousseau 2004; Foerster et al. 2007; Innocenti and Morrow 2010). Recent discussions question whether intralocus sexual conflict involving a single gene can be considered a “true” conflict of evolutionary interests or might instead be better described as an “evolutionary tension” from opposing selective pressures in each sex (Gardner and Úbeda 2017). We note that in the examples outlined below, the genetic basis is generally assumed to be underpinned by a single gene, but this is not usually known. Hence we retain the framework of intralocus sexual conflict here for convenience.

A gene controlling growth rate in both sexes could become subject to significant evolutionary tension if there were differing male and female optima for the optimal size at sexual maturity. Several experiments in fruit flies support

the existence of this form of interaction (Chippindale et al. 2001; Ruzicka et al. 2019). In these, the "same" genome is expressed in both sexes, and the fitness of each sex is then measured in a standardized manner. The findings suggest genomes that confer high fitness for adult males result in lower fitness when expressed in females, and vice versa (Chippindale et al. 2001; Ruzicka et al. 2019). Another approach has been to use experimental evolution experiments in which replicated lines of individuals are set up to experience different sexual regimes, with the evolutionary consequences of those environments measured after many generations have passed. In this way, researchers manipulated the genetic makeup in fruit flies to allow the genomes of either sex to evolve free of the constraint of passage through the other (Holland and Rice 1999; Rice 1992, 1996). The intriguing results of these experiments indicate the apparent evolution of genomes that confer higher fitness on the sex through which they had been solely transmitted. Thus, intralocus sexual conflict is predicted to lead to an evolutionary response and counter depending on the presence of specific alleles and extent of sex-biased gene expression (Hayashi et al. 2007; Parker 1979).

This type of scenario forms one of the two explanations that evolutionary biologists have sought for the stable persistence of homosexuality both in humans and in primates (Vasey et al. 2007). The first idea is centered in inclusive fitness benefits (Vasey et al. 2007, Vasey and VanderLaan 2010), the second in sexual conflict (VanderLaan et al. 2012). Homosexuality could be maintained through kin selection if homosexual individuals showed altruism to kin, with the result that sisters or brothers of homosexual individuals have more offspring than the average (Vasey et al. 2007; Vasey and VanderLaan 2010). However, the same effect could also occur via the effects of intralocus tensions, if homosexual males share genes for high female fitness with their sisters, with those genes having the effect of decreasing their own direct reproduction (VanderLaan et al. 2012).

An interesting question is how intralocus sexual conflict can be reduced or resolved. It has been proposed that one route is via the duplication of genes subject to intralocus sexual conflict, allowing them to take on new sex specific functions, or by the evolution of sex limitation—that is, silencing the expression of genes in one sex but not the other (Connallon and Clark 2011, 2014; Ellegren and Parsch 2007; Mank 2017b; Parsch and Ellegren 2013; Wright et al. 2018). Assuming that the evolution of sex-limited gene expression is preceded by sex-biased gene expression, or that sex-biased gene expression in one direction or the other indicates a lessening or increase in sexual antagonism, then it should be possible to detect the resulting signatures. This could be done by documenting

variation in, or manipulating the extent of, sexual conflict in a system and then testing for corresponding variation in sex-biased gene expression within the genome (Ellegren and Parsch 2007; Innocenti and Morrow 2010; Mank et al. 2013; Parsch and Ellegren 2013; Perry and Mank 2014, Wright et al. 2018).

Several studies have indicated that patterns of sex bias in gene expression can evolve rapidly, rendering their investigation experimentally tractable. The existence of high levels of sexual selection have been reported to lead to the evolution of stronger male-biased transcriptomes (Harrison et al. 2015; Hollis et al. 2014; Pointer et al. 2013). Hollis et al. (2014) working with *Drosophila melanogaster* fruit flies found that the experimental imposition of monandry (single-pair matings) over many generations led to a pattern of gene expression consistent with a move toward the female optimum, whereas polyandry (one female mating with several males) was associated with greater expression of genes associated with male benefit. Though generally consistent with the general expectations of sexual conflict, there are some exceptions (e.g., Veltsos et al. 2017). In general, our understanding of the fitness consequences of sex-biased gene expression remains incomplete. These studies also underscore the importance of investigating the range of natural mating patterns of the species under investigation. This is relevant to discussions of the proposed ancestral or natural mating patterns found in humans, which is explored further in this section.

The co-evolutionary dynamics predicted to result from intralocus sexual conflicts are unclear (Ruzicka et al. 2019; Schenkel et al. 2018). It should also be noted that the evolution of sex limitation by gene duplication or via the evolution of sex-limited gene expression is not necessarily an endpoint. For example, the evolution of sex-limited gene expression can itself result in fitness costs in the other sex and hence “move” the conflict instead to one that is now mediated between different loci (Chapman 2006; Chapman et al. 2003).

SEXUAL CONFLICT BETWEEN LOCI

In this scenario, the trait over which there is sexual conflict is influenced by different loci in males and females (Arnqvist and Rowe 2005; Kokko and Jennions 2008). For example, family size, or how much to invest in each offspring may be influenced by inputs from the actions of different genes in mother and father. Interlocus sexual conflict appears to be extremely common and evidence for it has been summarized in depth (e.g., Arnqvist and Rowe 2005; Chapman 2006, 2018; Chapman et al. 2003; Perry and Rowe 2015). It is often evidenced by manipulating the focal trait up and down and documenting the resulting opposing effects on fitness of each of each sex (Arnqvist and Rowe

2005; table 3.2). Classic examples of interlocus sexual conflict have been described in studies of pondskaters. In this, males gain more from a higher frequency of mating than do females. The evolutionary conflict over mating frequency between the interests of genes in males versus females has been revealed in experiments in which the grasping adaptations of males that aid in mating attachment are observed to become less effective in securing matings following experimental lengthening of antigrasping adaptations in females (Arnqvist and Rowe 1995). Further research across different pondskater species has revealed coevolutionary associations between the male grasping and female anti-grasping sexual morphologies, exactly as expected by theory (Arnqvist and Rowe 2002a, 2002b; Perry and Rowe 2012; Perry et al. 2017; Rowe and Arnqvist 2002).

Table 3.2 Types of Evidence for Sexual Conflict

Form of evidence	Description	Example
Economic—costs and benefit measurements	Data on the fitness effects of the sexually antagonistic trait on both sexes	Arnqvist & Rowe, 2005; Rowe & Day 2006
Experimental evolution	Studies of selection and counterselection in males and females; fitness consequences of the arrest of evolutionary processes in one sex but not the other	Rice, 1992, 1996
Genome-wide studies of fitness effects	Detection of sexually antagonistic genetic variation	Bonduriansky & Chenoweth, 2009; Brommer et al. 2012; Chippindale et al. 2001; Fedorka & Mousseau, 2004; Foerster et al. 2007; Innocenti & Morrow, 2010; Ruzicka et al. 2019
Patterns of genomic imprinting	Detection of parent or origin imprinting patterns of genes involved in mediating sexual conflict.	Haig, 2004, 2010
Molecular evolution—sequence comparisons	Description of patterns of molecular evolution and functions of reproductive proteins provide evidence for positive selection that is at least partly driven by antagonistic effects. Rapid turnover of sexual conflict genes among very closely related species, recruitment of such genes de novo. Evidence for coevolution between male and female reproductive proteins involved in mediating conflict	Begun & Lindfors, 2005; Begun et al. 2006; Clark et al. 2009; Haerty et al. 2007; Hart et al. 2014; Levitan & Ferrell, 2006; Swanson & Vacquier, 1995, 1998, 2002; Swanson et al. 2001a, Swanson et al. 2001b, Swanson et al. 2003
Comparative	Coevolution of morphological structures that mediate conflict. Assessment of divergence and speciation rates in groups in which conflict predicted to be high.	Arnqvist & Rowe 2002a, 2002b
Genomic	Analysis of sex-biased gene expression across species	Mank, 2017a; Wright & Mank,

	to provide signatures of sexual antagonism and the involvement of sex-specific gene regulation in resolving conflicts	2013, Wright et al. 2018

Interlocus sexual conflict could be resolved by selection for sex-specific gene regulatory systems to reduce the expression or effects of sexually antagonistic loci expressed in the other sex. One potential example comes again from the fruit fly *Drosophila melanogaster*. Here, females may frequently suffer costs of mating as a side effect of male adaptations to competition in this multiply-mating species (Chapman 1992, 2006; Chapman et al. 2003). Seminal fluid proteins (SFPs) transferred from males to females during mating can benefit both sexes but can incur costs in females, apparently reflecting the actions of interlocus sexual conflict (Chapman et al. 1995; Fricke et al. 2009b; Wigby and Chapman 2005). However, mating and the receipt of SFPs also stimulates the expression of a number of regulatory microRNAs in females (Fricke et al. 2014). The actions of these miRNAs can buffer against the costly effects of SFP receipt (Fricke et al. 2014; Green et al. 2016).

Similarly, studies of experimental evolution in *D. melanogaster* fruit flies have shown that females subjected over many generations to elevated levels of sexual conflict in male-biased adult environments can evolve resistance to the lifespan-shortening effects of exposure to males (Rostant et al. 2020; Wigby and Chapman 2004). Interestingly, this evolution of resistance is also condition-dependent, with females in poor condition due to nutrient limitation in adulthood being apparently unable to evolve it (Rostant et al. 2020). The mechanistic basis of this form of resistance evolution is as yet unknown, though it has been suggested that the very form of mechanistic pathways deployed by males to manipulate the reproductive systems of females may act to make the evolution of resistance in females more difficult to achieve (Chapman 2018). These studies also illustrate how the intensity of male–male competition can exacerbate the degree of sexual conflict with females (Arnqvist and Rowe 2005; Civetta and Clark 2000).

The predicted co-evolutionary outcomes of intersexual conflict are varied and include evolutionary chases, equilibrium, and divergence (Brockhurst et al. 2014; Hayashi et al. 2007) as well as reduced of the conflict (Arnqvist and Rowe 2005; Rowe et al. 2005). However, reduction of conflict in one arena does not necessarily resolve it completely if it continues via alternative routes (Rowe et al. 2005). Exactly how differences in these two underlying modes of sexual conflict interact and together determine the evolutionary outcome of sexual conflicts is also not yet clear (Pennell et al. 2016; Schenkel et al. 2018).

Sexual Conflict and Social Interactions

One of the themes we explore is the extent to which the enhanced capacity for social interactions in humans can impact upon the intensity of sexual conflict. Within a kin-selected context, or with strong inbreeding, we expect the intensity of sexual conflict to be significantly diminished due to the closer alignment of evolutionary interests between the interacting individuals (table 3.1; Faria et al. 2020; Parker 1979; Rankin 2011). Experiments in fruit flies have sought to test this idea by manipulating the relatedness of interacting males and females and testing whether conflicts are reduced when relatedness is higher (e.g., Carazo et al. 2014, 2015). Though some findings are consistent with this prediction (Carazo et al. 2014, 2015) others are not (Chippindale et al. 2015; Hollis et al. 2015), and, overall, the role and relevance of relatedness versus familiarity in these interactions within their natural context is not resolved (Chippindale et al. 2015; Hollis et al. 2015; Le Page et al. 2017; Martin and Long 2015).

However, many instances of social interactions take place within and between varied groups of unrelated males and females. We ask here whether this too impacts upon the intensity of sexual conflict. Again, in model systems such as fruit flies, this question has been addressed to some extent by studies that have experimentally modified the social environment and measured the impact upon the reproductive outcomes of the individuals involved. What is clear from this work so far is that the impact of different types of social groupings on individuals can be significant (Billeter and Levine 2013; Kent et al. 2008; Lymbery and Simmons 2017). Manipulation of the social environment of males and females can have significant effects on gene expression (Kent et al. 2008, Mohorianu et al. 2017, Mohorianu et al. 2018) and the reproductive success of both sexes (Bretman et al. 2009; Bretman et al. 2011a, Fowler et al. 2021a, 2021b).

For example, exposure of male *D. melanogaster* fruit flies to other males prior to mating causes significant, pervasive changes to the expression of genes in males (Mohorianu et al. 2017). Such males mate for significantly longer when they do meet a female and transfer more of key SFPs during mating (Bretman et al. 2009, Wigby et al. 2009). Males cue in to a combination of pheromonal, tactile, and auditory cues from other males (Bretman et al. 2011b), and functional memory is a core component of a male's capacity to respond (Rouse et al. 2018). By adjusting their reproductive effort to the presence of same-sex rivals, males significantly elevate their mate's fecundity, make her less likely to mate again, and father more offspring (Gage 1991; Gage and Barnard 1996;

Bretman et al. 2009; but see Dore et al. 2020). Male *D. melanogaster* also increases aggressive behavior toward rivals when the number of rivals is low but decreases aggression when high (Nandy et al. 2016). This results in an increased chance of mating when competition is low and decreases the risk of damage or diminishing fitness returns when competition is strong (Nandy et al. 2016). The extent to which the social responses of males in response to male–male competition appear to serve to exacerbate sexual conflict isn't yet known. However, the reported increased transfer of a SFP whose receipt can be costly to females from males following their exposure to rivals suggests it is possible (Sirot et al. 2011; Wigby and Chapman 2005; Wigby et al. 2009). In addition, the finding that males can qualitatively and quantitatively adjust their ejaculates in response to male–male competition highlights a fascinating level of male control, whose ramifications could be significant across many different species (Sirot et al. 2011; Perry et al. 2013; Wigby et al. 2009) including in humans.

Similarly, females exposed to other females prior to mating show decreased egg laying after mating (Fowler et al. 2021b). These changes occur in response to cues left behind by other females. Mating and the transfer of a key SFP from males during mating also cause females to become more aggressive (Bath et al. 2017; Chapman and Wolfner 2017). Thus the indicators used by both sexes of their sociosexual environment appear to vary considerably, potentially because the form of competition to which each sex is responding differs. Though the longer-term adaptive value of such responses in females isn't known, the results show that, like males, females are exquisitely responsive to their social and sexual environments (Dore et al. 2018).

Interestingly, the socially plastic responses of females and males also interact. The willingness of females to mate and their subsequent fecundity are determined by the interacting plastic responses of both sexes in both choice and no-choice scenarios (Fowler et al. 2021a). This indicates that the interacting plasticity of both sexes represents an important and novel facet of sexual interactions. Whether the socially plastic responses of either sex directly affect the extent of sexual conflict is not known. Though theory shows that plasticity expressed by both sexes could interact to increase the fitness of both (McGhee et al. 2013) or of one sex at the expense of the other (Day and McLeod 2018; McLeod and Day 2017; Yamaguchi and Iwasa 2015). The results of these experimental studies on the effects of the social environment show that its effects are significant, which suggests that further studies of its effects on the intensity of between-sex interactions is warranted across a wider range of taxa.

Sexual Selection, Sexual Conflict and the Study of Reproductive Interactions in Humans

Having outlined the major concepts and arenas for sexual conflict and outlined the types of evidence for them, we turn to the evidence for sexual conflict in humans. In this we are careful to emphasize that although evolved differences between males and females can be recognized, we do not equate them with inevitability of action or behavior.

Males and Females Have Different Reproductive Strategies

The imperfect alignment of evolutionary interests that is the hallmark of sexual conflict is apparent in humans, as in other sexual species (see section "Sexual Selection and Sexual Conflict—The Fundamentals"). As in other mammals, the initial investment in producing each offspring is greater in women than it is in men due to obligatory gestation and, for ancestral humans, obligatory lactation, and women often experience higher costs of reproduction from this and subsequent asymmetries in parental care. Many data support this contention. To draw on two examples, in a nineteenth-century Utah population, both mothers and fathers suffered depressed lifespan associated with an increased number of children, but costs for mothers were up to threefold higher (Penn and Smith 2007). Moreover, lifespan costs for women occurred not only in the period immediately following parturition, but continued into postreproductive life after age 50, whereas men experienced no increase in mortality from fatherhood after age 50 (Penn and Smith 2007). These costs within a population are mirrored in among-population patterns. Across societies, women generally outlive men, but men's lifespan gets closer to that of women as mean population birth rate increases, with mean birth rate explaining a sizable proportion (17 percent) of variation in the sex difference in lifespan across populations (Maklakov 2008).

As in many other animals, men often stand to gain more units of reproduction from acquiring multiple mates than do women. In the language of sexual selection, the Bateman gradient for human males tends to have a stronger slope compared with the female gradient, in those few populations for which data are available (Brown et al. 2009a; but see Borgerhoff Mulder and Ross 2019). Although there is much variation in how male–female relationships are structured across populations (Brown et al. 2009a; Schacht and Kramer 2019) a common feature of human mating systems is a male–female pair-bond, most typically expressed as serial monogamy (Schacht and Kramer 2019). Both the

higher costs of reproduction for women and the higher gains from mating for men lead to asymmetric reproductive investment per offspring and the potential for sexual conflict over mating and reproduction. These consequences set up a raft of opportunities for sex-specific selection throughout the human life cycle. These are explored in the next section focusing on events before, during, and after mating.

Precopulatory Interactions and Sexual Selection

There is ample evidence consistent with the idea that precopulatory sexual selection and sexual conflict have been important in the evolution of human mating behavior. There is clear competition within both sexes to acquire mates, and especially mates of high quality or reproductive value. Both sexes appear to attend to cues and signals of quality in the opposite sex and exhibit mate preferences and mate choice in relation to those cues and signals. Below, we discuss evidence for sexual conflict over mate choice and its consequences for human mating behavior, restricting our discussion to heterosexual mate choice.

MATE CHOICE IN HUMANS

The challenges of testing evolutionary hypotheses in humans are well known (e.g., Nettle et al. 2013). In studies of mate preference and choice in other animals, the strongest approach is a phenotypic engineering study in which a putative preferred trait is experimentally altered and mating preference and success subsequently measured in natural populations. It is impossible to ethically conduct exactly this study with humans, or indeed with many animals, so creative alternatives are needed, along with an awareness of study limitations and alternative hypotheses. The next best alternative is often to combine a demonstration of a mate preference in a controlled setting with a measurable correlation between mating success and a preferred trait in natural populations, while statistically controlling for potentially confounding variables.

Despite the challenges, there is abundant evidence that both sexes are choosy about their mates (Buss and Schmit, 2019). It is clear that females prefer men with certain traits, when offered a choice in controlled studies. It is also clear that individuals with some preferred traits achieve a higher likelihood of attracting a mate, attract more mates, and attract higher-quality partners (i.e., with more potential for future offspring production). It is often more difficult to directly connect mating preferences to realized partner choice and higher reproductive success by preferred mates in natural populations; that is, to show that specific mate preferences manifest in a multidimensional mating market in

which both sexes choose based on multiple traits and are constrained in their choices. Likewise, it is seldom clear that individuals with certain traits achieve higher mating success because of those traits (vs. a positive correlation with other causal traits) and because of mate choice by the opposite sex (as opposed to intrasexual competition). It is also difficult to determine whether women (and, to a lesser extent, men) exhibit mate preferences because preferred mates provide direct benefits (e.g., parent investment and the avoidance of disease transmission, sperm health, and fertilizing ability) or indirect benefits (e.g., high-quality genes transmitted to offspring). An important and under-appreciated point is that direct and indirect benefits are intertwined. A male that provides direct benefits because he is free from parasites might have evaded parasites through his good genes.

Many studies have identified traits in men that women prefer, in experimental studies that manipulate a focal trait while controlling for other factors, and in studies of natural interactions in which focal traits co-occur with other variables (e.g., dating profiles on matchmaker sites). In general, women prefer traits associated with direct benefits from a male's ability to invest in offspring through providing resources or engaging in parental care (Buss 1989, 1994; reviewed by Buss and Schmitt 2019; Geary et al. 2004). For example, women rate men in photographs as more attractive if they appear to cooperate with a child (Brase 2006). In a study of "lonely hearts" newspaper dating profiles, women preferred profiles that signal family commitment and resources (e.g., financial status and occupation; Bereczkei et al. 1997), consistent with evidence across cultures that women value male ability to provide resources (Buss, 1989). Both resource provision and parental care are consistent with direct benefits, but they are also consistent with indirect benefits, since males who acquire more resources or have the ability to invest in parental care might be able to do so because of their high genetic quality (in the sense that their alleles are a good fit to their current environment, or might provide higher sperm quality and fertilizing ability; Jeffery et al. 2016).

Women also prefer a wide range of male traits that are not directly related to resource provision or parental care, but that might be indirectly related to resources and care or might relate to high genetic quality. Women's preference for male height is well-documented (reviewed by Courtiol et al. 2010) and is largely consistent across cultures (Sorokowski et al. 2016). Women prefer experimentally lowered male voices (Feinberg et al. 2005), men who appear to have more upper body strength (Sell et al. 2017), men with specific body odors (Wedekind et al. 1995), and men who appear to display kindness (Lee et al. 2015). Some male features that women find attractive are also correlated with

nonmating performance. *Tour de France* cyclists that women rated as more attractive from facial photographs performed better in the race (Postma, 2014). This might mean that endurance has been an important quality in male mates in our evolutionary past (e.g., Bramble and Lieberman 2004), or that facial attractiveness is associated with good health which both allows high endurance and provides direct (e.g., sperm health and fertilizing ability) or indirect (good genes) benefits.

Despite the complexities of the mating marketplace, in which the realization of mate preference depends on the strength of competition for mates and the chooser's own relative mate value, there is plenty of evidence that males with preferred characteristics achieve higher reproductive success. Male resource-provisioning status (measured through, for example, hunting ability, wealth, or political influence) is positively associated with reproductive success (e.g., number of surviving offspring) across nonindustrial societies (von Rueden and Jaeggi 2016). But considering the case of male height illustrates just how challenging it is to interpret population-level patterns. Male height is positively associated with offspring production (Pawlowski et al. 2000; Stulp et al. 2015), a pattern that is sometimes attributed to active selection for height by women (Pawlowski et al. 2000). But it is difficult to rule out the possibility that a third factor explains both height and offspring production (e.g., there are positive associations between height, intelligence (a preferred trait itself) and income; Keller et al. 2013; Prokosch et al. 2009). Indeed, in a Dutch population, taller men had higher reproductive success despite finding partners later and producing their first child later, suggesting that they might not achieve higher reproduction through being preferred by women (Stulp et al. 2015). The relationship between height and reproductive success is further complicated by the assortative pairing for height that is common across populations (Stulp et al. 2013). Short men often partner with women who have lower scores for mate quality (Stulp et al. 2014) and less education (Ponzo and Scoppa 2015), such that reduction in reproductive success with short stature might result from partner characteristics rather than being disfavored mates. All of these factors are likely to be interrelated, such that sexual selection via female preference might disfavor short men, who both achieve fewer matings and partner with less reproductively productive mates, and short stature might be associated with other traits disfavored by females, including health, which might itself reduce offspring production.

There can be little doubt that women prefer mates with certain characteristics, that they exercise those preferences within the constraints of the mating marketplace, and that males with preferred characteristics have higher reproductive success as a result. But nailing down the ways that mate choice is

constrained, the selective pressures acting on female preferences and the magnitude of selection on male traits via female choice versus other selection remains a major challenge.

We can also expect mate choosiness in men. Males of any species should exhibit mate preferences when males are limited in their mating rate and females vary in their quality (i.e., their ability to produce offspring; Bonduriansky 2001). Both conditions appear to be met in humans. Of course, the existence of male mating preference does not mean that males are not strongly selected to achieve higher mating rates. Male mate preferences exist even in species with strong positive selection on male mating rate (Edward and Chapman 2011, e.g., in the fruit fly *D. melanogaster*; Bateman1948; Byrne and Rice 2006; Edward and Chapman 2012, 2013a, 2013b) and the cricket *Gryllus bimaculatus* (Han et al. 2020).

Laboratory studies demonstrate male preferences for female traits associated with fertility and caring ability or intent (Buss, 1989; reviewed by Geary et al. 2004). Men prefer female partners who are sexually mature, younger than themselves, and relatively slender (Brooks et al. 2015; Buss 1989; Crossley et al. 2012; Hume & Montgomerie 2001). All these characteristics can be viewed as cues of reproductive potential. Although there is consistency in preference across human populations (Buss 1989; Brooks et al. 2010), there remains much room for nuance. The form and magnitude of male preference are sensitive to the environment (e.g., the operational sex ratio), integration across multiple female traits, and the state and motivation of the chooser (e.g., Geary et al. 2004, Lee et al. 2015). These studies of human mate preferences offer lessons for the study of other animals, where variation in mate choice with individual state and experience and the environment, is sometimes overlooked.

There is also evidence that men's mate preferences translate into mate choice in natural populations. Male preference for high female fertility is consistent with human age differences in marriage, whereby husbands are on average older than wives (Buss 1989; Geary et al. 2004; Kenrick and Keefe 1992). Men who prefer slimmer women have partners who are slimmer than average (Courtiol et al. 2010). Taller men tend to mate with more educated partners (Ponzo & Scoppa 2015), consistent with the idea that more preferred mates obtain more valuable mates in the opposite sex.

We have highlighted only a few examples from the vast literature on human mating preferences and choice. Collectively, these findings demonstrate complexity in mating preferences, and the translation of preferences into mate choice is further complicated by environmental variation, the multidimensional mating market, and social learning and cultural effects on mate choice. Yet, the

fact remains that men and women appear to have mating preferences, and to act on those preferences, in ways consistent with sexual selection theory. Mating preferences set up the potential for sexual conflict between preferred and nonpreferred mates, which we address in the following section.

SEXUAL CONFLICT OVER MATING

Because men and women experience different costs of reproduction and often of mating itself, we should expect a fundamental conflict over mating in humans, as in other animals as seen in the section "Sexual Selection and Sexual Conflict—The Fundamentals." Sexual conflict represents a powerful source of selection that will favor male traits that overcome female reluctance to mate—through persuasion, harassment, or coercion—and corresponding selection for female traits for evading male detection and resisting male mating efforts (see Camilleri, this volume). Further conflict arises over mate choice between low-quality or disfavored mates of either sex and preferred mates of the opposite sex. This form of conflict should likewise select for persistence traits in low-quality mates, including deception, and resistance traits in high-quality mates, including mate scrutiny and the detection of deception. We emphasize that traits that arise in response to sexual conflict are not limited to direct aggression toward the opposite sex (though this also arises (Buss & Duntley 2011) but can include courtship and display traits, along with any other traits arising from the evolutionary conflict of interest between males and females or between preferred and nonpreferred mates.

It is difficult to distinguish biological adaptations from culturally permitted behaviors. Nevertheless, there are plenty of examples of human male behavior that are consistent with persistence in response to sexual conflict over mating, both in the acquisition of new mates (e.g., male harassment of nonpartner women) and over mating behavior within partnerships (Buss 2017; Camilleri and Quinsey 2012). As examples, men exhibit mate guarding that is consistent with conflict over mate choice by their partners (Buss 1988; Gangestad et al. 2005). Men are reported as more likely than women to suspect infidelity by their partners (Paul and Galloway 1994, reviewed by Camilleri and Quinsey 2012) and exhibit more frequent vigilance of their partners when partners are fertile (Gangestad et al. 2002). A resistance trait in women might take any of several forms, including traits for evading male detection, subverting male control of mating decisions, mitigating harm from male harassment, detecting deceptive signals from low-quality males, and behaviors that screen out low-quality mates. Observations of women displaying traits like these are consistent with resistance to male harm or manipulation. For example, women are more likely to pursue

extra-pair copulations during the preovulatory fertile period, consistent with seeking fertilizations from nonpartner men (Bellis and Baker 1990). Remarkably, women appear able to accurately predict unfaithful sexual behavior within partnerships from photographs alone (Foo et al. 2019), based on facial cues of masculinity (Foo et al. 2019; Leivers et al. 2015; Rhodes et al. 2012) that are correlated with seeking short-term partnerships (Boothroyd et al. 2008).

In dance flies, females inflate their abdomens to attract males by falsely signaling a high egg-laying (Funk and Tallamy 2000). Similarly, efforts by human women to manipulate male perception of their fertility and caring intent (e.g., to appear younger and more slender; Davis and Arnocky 2020)) are consistent with deception of partners about their mate quality. These traits can be understood through the lens of sexual conflict over mate choice between low- and high-quality partners. As in other animals (Long et al. 2009), females that signal high fertility might attract too much male attention in populations in which male harassment is costly for females, which would reduce selection for the deceptive exaggeration of signals of fertility (or alternatively select for mating signals to be "narrow-" rather than broad-cast).

Sexual conflict can lead to coevolution between the sexes (see section "Sexual Selection and Sexual Conflict—The Fundamentals"), which might take the form of an escalating arms race. There is, in fact, little direct evidence for sexually antagonistic coevolution between men and women, but there is also little direct evidence for it in other species (Perry and Rowe 2018). Instead, researchers have sought evidence in terms of its resulting footprints (Rice et al. 2012, 2013, 2016). It remains unclear whether persistence and resistance traits in each sex evolve in response to evolutionary change in the other, as in true coevolution, whether each sex evolves towards its own optimum independent of evolved changes in the other, or whether one sex adapts to its local environment and the other sex evolves to chase it in evolutionary space. Discriminating these alternatives is challenging.

Postcopulatory Interactions

There is evidence for a rich suite of postcopulatory interactions shaped by sexual selection. This is discussed in depth in Starratt and Shackelford (this volume) and we summarize this topic only briefly here.

Human male ejaculates appear adapted to sperm competition, sexual conflict, and related selective pressures, as observed in animals. Supporting evidence comes from data on the rapid evolution of male reproductive genes (Andres et al. 2006; Braswell et al. 2006; Clark and Swanson 2005) and on the plastic

adjustment of ejaculates consistent with adaptive hypotheses (Kilgallon and Simmons 2005; Joseph et al. 2015; Leivers et al. 2014; Pizzari and Parker 2010; but see Pham et al. 2018). It is also conceivable that biased reproductive decisions might occur after mating via a process known as cryptic female choice. This could occur if women bias fertilization toward preferred partners, if follicular fluid shows differential effects on sperm (Ralt et al. 1991), or if interactions between male and female identity influence how strongly sperm is attracted to follicular fluid from different women (Fitzpatrick et al. 2020). Women might also make other adaptive fertilization decisions postcopulation. Parental investment theory predicts that, in some circumstances, females that have relatively low ability to invest in offspring—through their own qualities or their partners' qualities—should invest in daughters, while females that are amply able to invest in offspring should invest in sons (Trivers and Willard 1973). Consistent with this, women who experience substantial stress loads—one possible measure of parental investment ability—have fewer sons (Ruckstuhl et al. 2010, Walsh et al. 2019).

Sex Chromosomes and Sexual Traits

Various evolutionary conflicts arise through the sex-specific inheritance of the sex chromosomes (Fry 2010; Gardner and Úbeda 2017; Rice 1984). Any of these conflicts should apply to the evolution of human phenotypes. Here we highlight one.

Evolutionary conflict arises because the sex-specific inheritance of the sex chromosomes generates differential genetic relatedness for X (or Z) chromosomes and autosomes between grandparents, parents, and offspring (Chrastil et al. 2006; Fox et al. 2010; Rice et al. 2010). For example, paternal grandmothers pass on an X chromosome to sons. In the next generation, that X is passed on to a son's daughters, but not to a son's sons. Taking the perspective of a locus residing on an X chromosome and expressed in a paternal grandmother, that locus can be confident of high relatedness to granddaughters ($r = 0.50$, as high as between parent and offspring), but equally confident that it has zero relatedness to grandsons. This marked imbalance in relatedness has potentially powerful consequences. Selection should favor X-linked genes expressed in grandmothers who devote resources to paternal granddaughters at the expense of paternal grandsons, and indeed even genes that harm paternal grandsons if resources are reallocated to granddaughters (Chrastil et al. 2006; Fox et al. 2010; Rice et al. 2010). Other evolutionary forces should counter this selection. The autosomes of paternal grandmothers do not experience this relatedness

imbalance, setting up a secondary conflict between X chromosomes and autosomes, and autosomes should experience selection to counter any efforts by X-linked genes to favor granddaughters or disfavor grandsons. Any helping or harming loci would evolve most easily if their expression is limited to paternal grandmothers. However, the discrepancy in relatedness is enormous, so the corresponding selection must be strong. It is likely that our species is one of the few in which we can expect this prediction to hold, because we are one of only a few species in which grandparents frequently care for grandchildren.

Population-level evidence is consistent with the prediction. The presence of a paternal grandmother in a grandson's life is associated with decreased childhood survival in six of seven societies (Chapman et al. 2018; Fox et al. 2010; Jamison et al. 2002; Rice et al. 2010). In another study, women provide more care for the children of daughters than for the children of sons (Danielsbacka et al. 2011). It sometimes seems that this astonishing and repeatable result does not receive the weight it deserves, and it is worth emphasizing that the relatedness difference occurs at the locus level (50 percent vs. 0 percent) rather than averaged across the entire genome (27 percent vs. 23 percent; Chapman et al. 2018; Rice et al. 2010. As always, in our species, it is difficult to rule out the possibility that cultural factors explain the pattern, but its occurrence across multiple societies lends more weight to the result. It would be most interesting to test the predictions in the few other species with grandparental care (Péron et al. 2019). If the result is correct and repeatable, it suggests that the autosomes consistently lose the evolutionary conflict over grandparental care, and that autosomal outnumbering of the sex chromosomes does not make up for the greater selection generated by the relatedness differential.

The sex chromosome-related conflict hypothesis offers a distinctly grim explanation for the evolution of menopause and grandmother care in humans. Perhaps grandmothering evolved not for its potential to help grandchildren but for its potential to help paternal granddaughters at paternal grandsons' expense, or more darkly, for its potential to harm paternal grandsons so that paternal granddaughters can prosper (Fox et al. 2011). Differences in relatedness of similar or smaller magnitude have driven the evolution of equally extreme behavior in other species (Székely et al. 2012).

Epigenetics and Conflict

Several fascinating forms of sexual conflict in humans are thought to be mediated through the expression of epigenetic marks. One conflict arises between parents of one sex and their opposite-sex offspring, and occurs over

epigenetic marks that regulate sex-specific development (Rice et al. 2012). Male and female mammalian embryos face the problem of how to develop along sex-specific pathways, an intralocus sexual conflict (see section "Sexual Selection and Sexual Conflict—The Fundamentals"). Part of the solution is that male fetal testes secrete androgen hormones that set development on a male trajectory. But sex differences in androgen secretion are inconsistent throughout fetal development, and absent in very early embryonic development before fetal gonad development. Yet, male and female fetuses do exhibit consistent sex-specific gene expression, including during the preandrogen stage. How is this accomplished? Rice et al. (2012) conjectured that fetuses employ epigenetic marks that depend on the sex chromosome complement to achieve the appropriate sex-specific expression of genes critical to male or female development. Such marks are indeed known in mammalian embryos (Bermejo-Alvarez et al. 2011). In early development, they allow sex-specific developmental trajectories in the absence of androgen signaling and in later development they increase sensitivity to testosterone in XY embryos and decrease it in XX embryos.

These sex-specific epigenetic marks solve the problem of intralocus conflict over sex-specific development, but a new problem is (sometimes) created. Epigenetic marks are normally erased between generations, but sometimes errors occur such that marks are not erased, and this can occur in a tissue-specific manner (Morgan and Whitelaw 2008). No problem arises if an embryo inherits unerased marks from a same-sex parent. However, when embryos inherit marks from opposite-sex parents, there is the potential for tissues to develop with sensitivity to testosterone that is mismatched to other tissues. Hence, the imperfect erasure of epigenetic marks generates sexual conflict between a parent —who gains from appropriate sex-specific development—and its opposite-sex offspring (Rice et al. 2012).

If correct, this hypothesis suggests an association with the occurrence of homosexuality and transgender identity in animals, including humans (Rice et al. 2012, 2013, 2016). An association with homosexuality would arise when sex-specific epigenetic marks attached to loci encoding sexual preference are carried across a generation to an opposite-sex offspring, resulting in mismatch between sexual preference and gonads. Transgender identity could likewise arise through mismatch between sexual identity and gonad identity. Supporting evidence for the hypothesis has accumulated. It can explain both the failure to detect genetic markers (Ngun and Vilain 2014) and the association of epigenetic markers with homosexuality, along with the occurrence of differences in sexual preference and identity in identical twins (Watts et al. 2018). It can also account for the strong

sex-specific effects of epigenetic disruption on development and behavior in other animals (Kundakovic et al. 2013), along with the widespread occurrence of same-sex sexual behavior across animals (Bailey and Zuk 2009). The hypothesis is not specific to humans, so future studies exploring epigenetic effects on same-sex sexual behavior in nonhuman animals would be valuable (Rice et al. 2012).

It is worth noting that the hypothesis that homosexuality is associated with epigenetic mismatch is consistent with adaptive hypotheses for the evolution of homosexuality (Bailey and Zuk 2009; Sommer and Vasey 2006). The stringency of erasure of sex-specific epigenetic marks might itself be subject to selection, such that selection favoring same-sex sexual behavior (e.g., Lerch and Servedio 2021) would tend to reduce its stringency.

Intralocus Conflict

The ingredients for intralocus conflict are the expression of shared genes in both sexes and selection acting in different ways on those genes (see section "Sexual Selection and Sexual Conflict—The Fundamentals"). Both conditions appear to be met, with more or less strength of support, for many human phenotypes. Many phenotypes expressed in men and women are generated from the same loci in both sexes, and it is likely that many of these phenotypes are under sex-specific selection. Examples include facial masculinity (Mitchem et al. 2014), hip width (Rice and Chippindale 2001), the timing of puberty (Cousminer et al. 2017), and lifespan (Archer et al. 2018). Other sex-limited phenotypes are generated from genes expressed in both sexes, such as polycystic ovary syndrome (Casarini et al. 2016).

The part that is often missing is direct evidence of current sex-specific selection acting on loci expressed in both males and females. A notable exception comes from data collected from an American population for the Framington heart study (Dawber et al. 1951). The study found that selection acts differently on men and women for several traits, including age at first reproduction, blood pressure, and height (Stearns et al. 2012). To the extent that genes contributing to these traits are shared between the sexes, we can conclude that there is ongoing intralocus conflict. Yet, it is not easy to extrapolate backward to what selection must have been like in past environments, which is what we need to know to evaluate how important intralocus conflict has been as a constraint in the evolution of human sexual dimorphism. Studies in other animals suggest that intralocus conflict is less likely in harsh or changing environments, in which selection acts congruently on both sexes as they evolve toward a new adaptive peak (Long et al. 2012). Intralocus conflict is more likely

in benign environments with weak selection, such as, so there are grounds to suspect that selection measured now does not reflect our recent evolutionary past. Nor is it easy to extrapolate forward to predict the extent to which intralocus conflict constrains future evolution. In the analysis of the Framington study, sexually antagonistic selection was detected through multivariate selection arising from genetic correlations among the focal traits investigated (Stearns et al. 2012). Measuring these correlations is essential to accurately predict the evolutionary trajectory for each sex, but what hope is there of accurate prediction when there will always be many unmeasured phenotypes?

Whether or not intralocus conflict has been fully resolved remains unknown for many human traits. It is clear that genetic correlations between the sexes can constrain evolution in the short term (e.g., Griffin et al. 2013). However, it is also evident, from abundant sexual dimorphism across the tree of life, that in the long term, selection can often break the constraints imposed by genetic correlations between the sexes. Careful study will be needed to determine whether genes shared by the men and women represent ongoing constraint through intralocus conflict or loci under congruent selection in both sexes.

Sexual Conflict and Cognitive Function

In concluding, we briefly address what might be the effect of dominant features of human society on the expression of sexual conflict. Specifically, we ask whether the higher level of cognitive function in humans is associated with a qualitatively or qualitatively different expression of sexual conflict. Dominant distinct features of human societies are culture and language. Whether these can exacerbate or diminish sexual conflict versus cooperation requires further investigation (e.g., (Boyd and Richerson 2005; Boyd et al. 2011; Feldman et al. 1985; Henrich 2004; Lehmann et al. 2008), though it does appear that, if anything, cultural evolution can lower the degree of cooperation expressed (Lehmann et al. 2008). Traits such as humor and personality type that may contribute to mate choice in humans may also have the potential to exacerbate conflict (Buss, 1989). Some researchers suggest that humans do not seem to be more cooperative than other animals (West et al. 2011) though the ability to form coalitions that require high levels of coordination may facilitate specific features of human conflicts such as intergroup warfare. What humans may have is an enhanced ability to gather information and precisely calibrate costs and benefits and punishments (Fehr and Gächter 2002; West et al. 2011). This would seem to have the potential to exacerbate conflicts rather than diminish them. Reciprocity, or the type of cooperation that can occur between nonrelatives (Trivers 1971),

appears to be especially important in humans, presumably because we have the requisite high-level cognition, recognition, and enforcement mechanisms to allow it to operate (West et al. 2011). The punishment that can be part of the reinforcement of reciprocity could be important in the context of sexual conflict, but it is not yet clear. Also unknown is how is conflict in humans modified by monetary resources interacting with personality types. Future research on how traits such aesthetic and ethical judgment, which may have some genetic component, may interact with traits such as parental care will be of interest.

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CHAPTER
4

Extensions of Sexual Strategies Theory across Peoples, Cultures, and Ecologies

David P. Schmitt

Abstract

Evolutionary behavioral scientists have amassed considerable evidence that human mating psychology displays adaptive design, varying in functionally predictable ways across sexes, ages, and socioecologies. Much of this evidence comes from studies of preferential choice, focusing on the specific features, types, and quantities of romantic partners women and men most desire. Women's mate preferences center, in part, on cues to a man's ability and willingness to provide resources. These preferences are usually stronger among women in harsh environments, and among women who themselves are feminine, attractive, traditional, and heterosexual. Men's mate preferences center, in part, on cues to youth and fecundity. These preferences are usually stronger among men in cultures that are less safe, less healthy, and possess more pathogens, and are stronger among men who themselves are masculine, wealthy, and possess higher testosterone. Several concerns with cross-cultural comparisons of human mating psychology have presented challenges to evolutionary scientists. Ultimately, cross-cultural tests of hypothesized human mating adaptations provide the most evidentiary value when embedded in detailed theoretical rationale for *why* the mechanisms should generate predictable patterns at multiple levels—across individuals, across groups, across cultures, and across time.

Key Words: mate preferences, culture, ecology, sex differences, individual differences

Mating across Cultures Worldwide

Considerable evidence suggests that human mating psychology displays some of the hallmarks of adaptive design, such as varying in functionally predictable ways across sexes (Campbell, 2013; Mealey, 2000), across developmental stages and age-linked reproductive circumstances (Klímová et al., 2021; Owens et al., 2020), across varying levels of personal mate value and fitness-relevant personality configurations (Jonason et al., 2009; Lukaszewski et al., 2014), and across cultural contexts and socioecological conditions (Nettle, 2009a; Sng et al., 2017). Much of this evidence comes from studies of *human mate preferences*—the basic desires people have for mating with those possessing particular personal characteristics (Buss, 2016; Geary et al., 2004). Adaptive design also underlies the types of mating relationships men and women most desire (Buss & Schmitt, 1993; Lippa, 2009), the fundamental mating strategies they tend to pursue (Gangestad & Simpson, 2000; Henrich et al., 2012), and their ideal quantities of romantic partners (Hughes et al., 2020; McBurney et al., 2005). This chapter focuses on the reasons why features of mating psychology appear to functionally vary across cultural contexts and socioecological conditions. A general overview offers why, where, and when to expect significant sex differences in human mate preferences and their phenotypic expression.

Overview of Adaptive Mate Preference Variation

Most animals do not to reproduce randomly, exhibiting instead some form of discriminating or preferential mate choice (Alcock, 2001; Bateson, 1983). Peahens, for instance, preferentially mate with peacocks who possess the most elaborate trains (Petrie et al., 1991), female great bowerbirds prefer males who build elaborate structures strategically decorated with stones, bones, and shells (Kelley & Endler, 2012), and in several bird species (e.g., canaries, swamp sparrows, chestnut-sided warblers, chickadees, and blue tits), females preferentially sire offspring with males who display the most elite vocal skills (Byers et al., 2010). Among the great apes, female common chimpanzees prefer to mate with males who display higher social dominance (Klinkova et al., 2005), female mountain gorillas mate more often with males whose chest beats provide accurate evidence of larger body size (Robbins, 2003; Wright et al., 2021), and female orangutans (when nearing ovulation) mate cooperatively only with prime flanged males (Knott et al., 2011). Across the animal kingdom, the sexes of all known sexually reproducing species possess evolved psychologies that generate discriminating desires and preferential mate choices. Evolutionary psychologists

have hypothesized that humans may possess evolved mating psychologies, like other sexually reproducing species, including preferential desires for mating with certain types of individuals more than others (Buss, 1989).

Sexual strategies theory (Buss & Schmitt, 1993) provided the first broad-based theory of evolved human mating psychology, anchored in Darwin's (1871) theory of sexual selection and modern elaborations of it (e.g., Trivers, 1972). It combined an evolutionary psychology task analysis of the adaptive problems that ancestral women and men have faced, cross-cut with contextualizing human mating along the temporal dimension of short-term mating (e.g., casual sex and one-night stands) to long-term mating (e.g., marriage and extended committed pair-bonding). Based on this task analysis, sexual strategies theory proffered predictions about psychological design features women and men might possess that become differentially activated when pursuing short-term versus long-term mating. For example, men were hypothesized to prioritize cues to reproductive value when choosing long-term mates but to prioritize cues to immediate sexual access more when pursuing short-term mates. Psychological design features for the latter included the desire for a variety of different sex partners, letting little time elapse before seeking sexual intercourse, and subsequently the male sexual overperception bias (first described in Buss, 1994). Women were hypothesized to prioritize cues to a man's long-term trajectory of ability and willingness to contribute resources to them and their offspring in long-term mating contexts. In contrast, women were hypothesized to prioritize qualities such as immediate access to resources, securing mate insurance, and possibly good genes more in short-term mating contexts. Abundant empirical evidence has accrued over the past few decades that support many, but not all, of these hypothesized psychological adaptations (see Buss & Schmitt, 2019, for a review).

Sexual strategies theory was not advanced as a final or complete theory but rather provided a skeletal framework, anchored in the sound evolutionary biology of sexual selection theory, for additional hypothesis generation and modification. For example, Buss and Schmitt (1993) suggested that future work should focus on task analyses involving individual differences such as variation in mate value and socioecological differences such as variation in local sex ratios. Consequently, this chapter reviews many human mating adaptations and their context-sensitivities hypothesized and discovered since the original formulation of sexual strategies theory. In this sense, the current chapter provides important extensions and elaborations of sexual strategies theory, moving the science of human mating toward the goal of a more complete, nuanced, and comprehensive theory of human mating, adding importantly to the fundamental framework originally outlined in 1993.

Why Sex Differences in Mate Preferences?

Throughout our ancestral past, humans have been subject to selection pressures that likely resulted in psychological sex differences (Archer, 2019; Buss, 1995; Geary, 2010), including at least some sex-differentiated mate preferences (Buss, 1989; Kenrick et al., 1990; Symons, 1979). To believe otherwise, one would have to presume humanity experienced a confluence of three highly unlikely scenarios: (1) selective forces acting on humans must have fully eliminated all phylogenetic inertia from our lineage as mammals and primates pertaining to psychological sex differences (e.g., completely liberating humans from Bateman's principles (Brown et al., 2009) and principles of parental investment theory (Trivers, 1972, among others); (2) selective forces acting on humans must have aggressively rebuffed any and all sex-specific mate preferences from developing during our hundreds of millennia as mobile hunter–gatherers (Marlowe, 2003a; Walker et al., 2011); and (3) selective forces acting on humans must have steadfastly maintained a perfectly androgynous human mate preference psychology throughout the post-Pleistocene epoch (see Buss & Schmitt, 2019). It would defy everything known about evolution by sexual selection to maintain that selective forces have continuously and completely "wiped the gender slate clean" of psychological sex differences during the long path of human evolution (Buss, 1995; Stewart-Williams & Thomas, 2013).

What makes a gender-blank-slate view of human evolution especially improbable is that the comprehensive purging of all psychological sex differences would have had to occur while selection simultaneously sculpted *very* large differences in women's and men's physical bodies such as grip strength and vocal tone (e.g., humans have the *largest* such differences among the great apes; Hill et al., 2017; Puts, 2016; Schild et al., 2020), in facial morphology and body fat distributions (Chiappa & Singh, 2017; Kleisner et al., 2021), and in height and hirsuteness (Dixson et al., 2003; Stulp & Barrett, 2016). It would mean all psychological sex differences were purged while selection sculpted in humans prominent sex-linked traits such as concealed ovulation and conspicuous female breasts (Low et al., 1987; Steward-Williams, 2018), large sex differences in pubertal timing and senescence through menopause (Ellis & Bjorklund, 2005; Hawkes et al., 1998), and eliminated any and all sex-linked psychology related to pregnancy and lactation (Campbell, 2013; Hrdy, 1999). It would mean all psychological sex differences were purged while humans manifested culturally pervasive behavioral sex differences in patterns of hunting large fauna over long distances versus plant gathering and childrearing (Helfrecht et al., 2020; Marlowe, 2007; Murdock & Provost, 1973; Wood et al.,

2021), in selection-relevant marital patterns and reproductive skew (Brown et al., 2009; Schmitt & Rohde, 2013; von Rueden & Jaeggi, 2016), and in the many behavioral traits associated with young male syndrome (e.g., intensified age-specific mortality, physical violence, intrasexual aggression, and risk-taking; see Apicella et al., 2017; Kruger & Nesse, 2007; Wilson & Daly, 1985). Perhaps the largest psychological difference between men and women is the target sex to whom they are typically attracted (see Gangestad et al., 2000; Lippa, 20020 Schmitt, 2007), yet somehow selection completely obliterated all other evolved mating inclinations that might be functionally advantageous when one erotically prefers one sex more than the other? As Vandermassen (2011) has noted, "human males and females should have evolved to be psychologically identical, for example, is a theoretical impossibility, and, indeed, turns out to be untrue" (p. 733).[1]

The probability that selective forces throughout human evolution fashioned absolute psychological sameness of the sexes while simultaneously recapitulating many physical and behavioral sex differences that align humans with the rest of the mammalian kingdom is essentially zero (Stewart-Williams, 2018; Stewart-Williams & Thomas, 2013). Consequently, evolutionary psychologists have hypothesized that humans possess at least some sex differences in psychological design (Buss, 1995; Geary, 2010), including a limited number of historically fitness-enhancing mate preference adaptations (Buss, 2016; Schmitt, 2014). A few evolved mate preferences are expected to be sex-differentiated, with some expressed more strongly in women (e.g., preferences for cues to the ability and willingness to devote resources; Buss, 1989; Ellis, 1992) and others expressed more strongly in men (e.g., cues to youth and future reproductive value; Lassek & Gaulin, 2019; Sugiyama, 2015).

Beware the Toxic Tetrad

Evolutionary psychologists do not expect sex-differentiated mate preferences are invariably expressed in *only* one sex or the other, with all men and all women in every culture around the world differing in exactly same way when it comes to evolved mating desires (Thomas et al., 2020; Walter et al., 2020). Oddly, evolutionary hypotheses are often misconstrued or falsely portrayed in such a manner, as though preferential mate choice—if at all influenced by biological evolution—must be expressed in ways that are *gender-essentialistic* (i.e., *all* women must prefer mates who possess resource-related cues and *all* men must prefer youth-related cues; Dar-Nimrod & Heine, 2011; Prentice & Miller, 2006), profoundly *gender-dichotomized* (i.e., *only* women and *no* men will express

preferences for resource-related cues, whereas *only* men and *no* women will prefer youth-related cues; Carothers & Reis, 2013; Joel et al., 2015; Meynell, 2020), fully *biologically determined* (i.e., resource-related and youth-related preferences are *inevitable* and *entirely reducible* to sex-related biology; Rogers, 2011; Rose & Rose, 2000; Schmitz, 2010; Zagaria & Zennaro, 2021), and *cross-culturally invariant* (i.e., all cultures must have the *exact same size* of sex differences in expressed mate preferences; Smith, 2020; Zentner & Mitura, 2012). Within the realm of sex differences in mate preferences, fallacious nature–nurture thinking has been supplanted by a noxious stew of *toxic tetrad* thinking that fuses (and confuses) extreme visions of gender essentialism, gender dichotomization, biological determinism, and cultural invariance beliefs.

This regrettable descent into toxic tetrad thinking may have been facilitated, in part, from scholars and the public mistakenly categorizing evolved mate preferences as "innate" aspects of human psychology (Barrett, 2001; Tooby et al., 2005). Innate is an imprecise concept with at least 27 possible definitions within the evolutionary sciences ranging from "present at birth" to "not acquired" to "not learned" to "genetically determined" to "highly heritable" to "species-typical" (Mameli & Bateson, 2006, p. 177). The concept of innateness confuses more than it enlightens. Much like human sex differences in height, voice, strength, and intrasexual aggression (Puts, 2016), most human mate preferences are clearly not present at birth and are just as clearly influenced by developmental experiences linked to culture and socioecology, including aspects of social learning (Batres & Perrett, 2014; Boothroyd & Vukovic, 2018; Little et al., 2011; Sorokowski et al., 2014). Yet, just like height, voice, strength, and intrasexual aggression, the dynamic and changeable aspects of human mate preferences in no way necessitate that sex differences in their phenotypic expression are "not evolved" (see Kenrick et al., 2010; Schmitt, 2015).

Essential, dichotomous, determined, and statistically invariant views of human sex differences can have wide-ranging negative effects on individuals and societies (Saguy et al., 2021; Skewes et al., 2018), including deleterious effects on science itself (Del Giudice, 2021a; Frederick & Reynolds, 2021). Unfortunately, toxic tetrad views of evolved sex differences are not uncommon in the scholarly literature on human sexuality[2] (Del Giudice, 2021b; Shtulman & Schulz, 2008; Zagaria et al., 2020), as illustrated by the following published erroneous depictions:

- Zentner and Mitura (2012), on the topic of sex differences in mate preferences, asserted: "Of importance for an evolved-adaptation account, the [sex] differences should hold across variations in culture and social context" (p. 1176).
- Smith (2019) claimed that evolutionary psychologists assume psychological adaptations such as

mate preferences are "universal—that they are possessed by almost every member of our species, and that they transcend cultural and historical boundaries" (p. 40).

- Endendijk et al. (2020) noted, "Evolutionary theories … would predict that there are no differences in [sexual double standards] between countries. If these double standards evolved from adaptive gender differences in reproductive strategies, they would be universal and should be visible in all countries" (p. 166).
- Wood and Eagly (2002) typify toxic tetrad portrayals of evolutionary psychology as "the most developed essentialist theory of the origins of a broad range of sex differences" (p. 700).

In sum, evolved sex differences in human mating psychology are *not* required to phenotypically transcend all cultural and historical boundaries, or to "hold steady" across all cultures for all time, or to be present at birth or all developmental stages, or to be an "essential" aspect of each and every individual within each sex (see Schmitt, 2015, 2017).

Evolved Sex Differences Are Interactive by Design

As further elucidated in the next sections, evolutionary psychologists have for decades articulated clear *interactionist* expectations for human mating psychology, arguing our evolved mate preferences are specially designed to be impacted by dynamically changing individual, cultural, and socioecological inputs (Buss & Barnes, 1986; Gangestad & Simpson, 2000). This dynamic interactionism is not simply the additive influences of genes and environment (Oyama et al., 2001). Rather, mate preferences are jointly and reciprocally determined by multiple causes, are context-sensitive, and whatever genetic influences exist are contingent on cultural contexts and socioecological conditions (Kenrick, 2001; Kenrick et al., 2003). Evolutionary psychologists assume psychological adaptations "require environmental input at every stage of their development, from initial evolution to current activation" (Al-Shawaf et al., 2019b, p. 2). As Buss (1998) noted more than 20 years ago, evolved mechanisms such as mate preferences are "not blind or robotic, nor do they express themselves in invariant ways insensitive to context" (p. 24). Evolutionary psychology from its inception has been rooted the concept of evolved psychological mechanisms firmly within interactionism, context-sensitivity, and expected cultural variation (Tooby & Cosmides, 1992). To my knowledge, the scholarly literature most frequently demonstrating toxic tetrad thinking about sex differences arises not from evolutionary psychologists but from the rhetorical epithets and erroneous mischaracterizations about evolutionary psychology spun by its critics[3] (Curry, 2003; Dennett, 2017; Fine, 2005; Hagen, 2015; Kurzban & Haselton, 2006; Meynell, 2012). Among scholars with scientific training in evolutionary psychology, mate preference adaptations are rarely hypothesized to

be essential, dichotomous, determined, or culturally invariant with regard to sex (Buss, 1998; Schmitt, 2015).

To the contrary, much of the mate preference variation observed across sexes, individuals, cultures, and socioecological contexts is explicitly *anticipated* by evolutionary psychologists, a partial result of dedicated and adaptive special-design features, not bugs, in what is thought to be a highly interactionist human mating system (Buss & Schmitt, 1993; Luoto, 2019; Schmitt, 2016). Specifying the interactive design features of human mating psychology (e.g., revealing exactly how and why neurodevelopmental mate preference mechanisms react to some personal experiences and socioecological conditions more than others; Buss, 2016; Luoto et al., 2019) has given evolutionary psychologists better tools for interventions when seeking to alter the expression of mating psychology in men and women around the world (Turner & Machalek, 2018; Tybur et al., 2012). For instance, adaptationist approaches to mating psychology have been used to inform effective interventions for sexual aggression (Malamuth & Heilmann, 1998; McKibbin et al., 2008), poor relationship functioning (Buss, 2000; Roberts et al., 2010), and gendered aspects of mental health (Kennair, 2003; Nesse, 2015).

Why Do Individuals Differ in Mate Preferences?

A defining feature of humanity's evolved mate preferences is that our mating desires are *not* expected to be equally expressed across all individuals, across all ages, or across all members of the same sex at all times and in every situation (Buss, 1998; Gangestad & Simpson, 2000; Whyte et al., 2021). Evolved mate preferences emerge within dynamic developmental contexts and are specially designed to seek out and react to individual, dyadic, familial, cultural, and socioecological inputs (Lukaszewski et al., 2014; Weekes-Shackelford et al., 2007). Thus, humans are typically hypothesized to express mate preferences in ways that are designed to be responsive to an individual's personal developmental experiences and local socioecological circumstances.

Low (2005), for instance, noted how personal access to resources is especially pivotal for some women more than others, with poor nutrition leading to infecundability and greater loss of fetuses and children among women at the lower end of fertility. Among those women who accrue resources themselves, there also are inherent trade-offs faced with a woman's ability to give time and energy spent in caring for her offspring. Consequently, women's expression of mate preferences for resource-related traits, according to Low (2005), may be affected by women's resource availability and ability to receive nonpaternal help

in raising offspring (see also Buss, 1989; Buss & Barnes, 1986; Stone et al., 2008). This is just one example of why personal experiences and local circumstances matter in the phenotypic expression of evolved mate preferences.

In humans, emerging evidence also suggests mating psychology is influenced by genetic and neurodevelopmental variation within each sex (Ganna et al., 2019; Zietsch et al., 2012) and that similar psychological mechanisms influence sexual behaviors across other mammalian species (Luoto et al., 2019). For instance, individual differences in sociosexuality (i.e., general tendencies to seek short-term mates vs. long-term mates) have demonstrated moderate heritability (Bailey et al., 2000) and are further calibrated by developmental events and socioecological conditions (Arnocky et al., 2021; Lukaszewski et al., 2014; Schmitt, 2005). Given that women's and men's mate preferences tend to shift somewhat depending on whether they are seeking short-term or long-term mates (e.g., Buss & Schmitt, 1993, 2019), genetic and neurodevelopmental variation may be a key source of within-sex individual differences in expressed mate preferences. Indeed, direct tests of the heritability of mate preferences tend to support this view (Verweij et al., 2012; Zietsch et al., 2015), including genetic evidence of sexual selection playing a role in certain expressed mate preferences (e.g., women's preferences for tall, intelligent, creative men; Verweij et al., 2014). Using data from 4,625 twin individuals from the United Kingdom Adult Twin Registry, Zeitsch et al. (2012) found the highest heritabilities in human mate preferences were for indicators of parental investment (e.g., earning capacity) and genetic quality (e.g., physical attractiveness)—two categories of mate preferences central to this review.

To summarize, like all psychological adaptations, human mate preferences are most properly viewed as expressed within an interconnected web of individuals across time, each person with their own particular genetic inheritance, developmental experiences (including those experienced in utero; Berenbaum et al., 2018), and local socioecological circumstances. Each individual faces a lifetime of inherent trade-offs for strategically solving the many adaptive problems of mate choice, mate retention, and parental investment (Conroy-Beam & Buss, 2019; Li et al., 2002; Waynforth, 2001). Each individual exists within a local mating pool network, always in flux, whose members and motivations influence the adaptive contingencies of expressing stronger preferences for some traits while deemphasizing other desires (Cunningham et al., 2002; Penke et al., 2007). While the sexes may differ in some mate preferences, evolutionary psychologists also expect mate preferences to vary across individuals within each sex, including influences that emerge due to individuals inhabiting different cultures and socioecologies.

Why Do Cultures Differ in Mate Preferences?

Evolutionary psychologists have hypothesized that some psychological adaptations adaptively respond to developmental experiences and socioecological factors, in so doing demonstrating behavioral plasticity via reaction norms (Dingemanse et al., 2010; Luoto et al., 2019), facultative adaptation (Schmitt, 2015), or socioecologically generated "evoked culture" (Gangestad et al., 2006). Among the environmental factors or inputs shown to most impact human mate preferences are key developmental experiences (e.g., growing up with resource scarcity, harshness, or unpredictability; Ellis et al., 2009; Garza et al., 2021), assessments of current condition (e.g., high vs. low personal mate value; Edlund & Sagarin, 2010; Millar et al., 2018), features of the local mating pool (e.g., male- or female-skewed sex ratios; Arnocky et al., 2014; Stone et al., 2007; Walter et al., 2021), local pathogen levels (Gangestad & Buss, 1993; Lee & Zietsch, 2011; cf. Walter et al., 2020), local mortality levels (Cohen & Belsky, 2008; DeBruine et al., 2010), among many other cultural contexts and socioecological factors (for reviews, see Low, 2007; Pisanksi & Feinberg, 2013; Sng et al., 2018).

Many psychological adaptations, including mate preferences, are also culturally influenced by selective social learning mechanisms (Apicella et al., 2007; Boothroyd et al., 2016; Little et al., 2011), in terms of both content-biased learning (e.g., men may find it easier to learn to prefer cues to youth than cues to old age; Cunningham et al., 1995; Miller & Todd, 1998) and target-biased learning (e.g., humans may learn mate preferences due to high-status prestige bias, biased mate copying from those with better access to critical information about potential mates, or biased learning from same-sex targets; Street et al., 2018). Any cultural variations in content-bias or target-related preference learning could be amplified over time by selective social learning. Indeed, many mate preferences are expected to have coevolved alongside cultural norms, beliefs, and practices that have culturally evolved themselves in ways that functionally impact the expression of human mating psychology (Price et al., 2014). Norms related to monogamous marriage, for instance, may have culturally coevolved alongside increases in the importance of men's resource-generating ability, men's willingness to invest within singular pair-bonded marriages, and reductions of sex differences in age-related mate preferences (Henrich et al., 2012).

Why Cultural Variation in the Size of Sex Differences?

Some cultural or socioecological factors may impact the expression of mate

preferences more profoundly within one sex than the other (or affect the links between individual differences and mate preferences within one sex more than the other; see Schmitt, 2015). This can result in the *size* of differences between women and men varying around the world, not because the sex differences are "not evolved" (as Zentner & Mitura, 2012, mistakenly conclude) but rather because our sex-specific adaptive design generates greater responsiveness to local circumstances in one sex more than the other.

For example, across most cultures men are, on average, taller than women (Gray & Wolfe, 1980). Across 76 "aboriginal" populations from the *Ethnographic Atlas*, Holden and Mace (1999) found sex differences in height ranged from 4 percent to 10 percent. Height is affected by exposure to poor nutrition during child development. However, poor nutrition affects boys' height growth significantly more than girls' height growth, resulting in sex differences in average adult human height that are conspicuously smallest in cultures with the poorest nutrition (Lippa, 2009). As Gaulin and Boster (1992) noted, "substandard nutrition could cause individuals to fall short of their genetically set growth potential, and, importantly, males seem to be more sensitive to such developmental perturbations than females" (p. 474). This suggests that height may be a condition-dependent sexual trait in men but not necessarily in women (see Krams et al., 2019; Rubika et al., 2020). It is also clear that parents sometimes discriminate in the nutrition they provide to sons versus daughters. Holden and Mace (1999) found suggestive evidence that parents facultatively invest more nutrition in daughters within cultures where women contribute more to subsistence (e.g., sub-Saharan Africa), and further documented that sex differences in height are minimized within these populations. So, although sex differences in height are not invariant in size across all cultures (e.g., being smaller in sub-Saharan Africa and larger in Scandinavia compared to the rest of the world; Schmitt, 2017), this in no way establishes that sex differences in height are "not evolved" or not influenced by biological adaptations of some kind (Nettle, 2002; Stulp & Barrett, 2016).

In a similar manner to height and mate preferences, many sexually selected traits appear to be especially stunted within poor cultural or socioecological contexts. As Geary (2017) has extensively documented, sexually selected traits in humans are among the most vulnerable traits during development, often requiring more energy to build, maintain, and phenotypically express. Hence, poor developmental experiences and socioecological conditions (e.g., high pathogens, psychosocial stressors, and nutritional deficits) and other ontogenetic perturbations tend to significantly reduce mental rotation ability and visuospatial tracking ability in men more than in women (with men generally being better at

these abilities), whereas poor developmental conditions tend to reduce face processing, verbal learning, and theory of mind abilities in women (but less so in men; see also Geary, 2021; Hone et al., 2020). Evidence suggests that several developmental or socioecological factors (e.g., general health, mortality, pathogens, and sex ratios) impact men's and women's phenotypic mate preference expression differently, as well (De Barra et al., 2013; DeBruine et al., 2010; for a review, see Schmitt, 2014).

Sometimes this impact on the size of sex differences may be *by design*, but sometimes it is not. An underappreciated nuance in this literature is the crucial distinction between sex differences in mate preferences varying in size across cultures due to size-specific facultative adaptations—mechanisms specially designed to evoke these precise levels of sex differences via mating psychology shifts—versus sex differences in mate preferences varying across cultures for nonadaptive reasons, for reasons related to adaptive mate preference shifts providing more fitness payoffs within one sex than the other, or for reasons that are mere side effects of other nonmate preference adaptations. For instance, reduced sex differences in height may result from poor nutrition affecting boys more than girls, but the minimized *degree of sex difference* in height observed in low nutrition cultures may not be an adaptation itself (Schmitt, 2015). Similarly, some religious adaptations may be specially designed to suppress certain aspects of women's mating desires and behaviors more than men's (Blake et al., 2018), but the attenuation or accentuation of the degree of sex difference in mating may not be the intended functional outcome per se (Schmitt & Fuller, 2015; see also McCullough et al., 2012). Specific *sizes* of psychological difference between men and women are probably seldom, if ever, the intended fitness-enhancing outcome of evolved mechanisms.

Still, cross-cultural shifts in the size of sex differences may have significant associations and impacts on fitness-related outcomes. For example, changes in the size of sex differences in height may affect processes of sexual selection across populations (Guo et al., 2018; Stulp & Barrett, 2016), and changes in women's activated mating desires and behaviors (e.g., related to short-term mating) across populations may affect expressions of jealousy, mate retention, mate guarding, degree of polygyny, and so forth (Bendixen et al., 2015; Schmitt & Rohde, 2013). All these issues involving mating psychology shifts across sexes, individuals, cultures, and socioecological conditions are pertinent to the first category of mate preferences covered in this chapter—women's long-term mate preferences.

Women's Long-Term Mate Preferences

Given the exceptionally high levels of paternal investment in humans compared to other primates (Geary, 2000), along with the relatively higher levels of obligatory maternal investment relative to paternal investment (Symons, 1979), evolutionary psychologists have hypothesized that women seeking long-term mates (i.e., an enduring pair-bond or marital partner) will especially desire those partners who display cues to the *ability* and *willingness* to devote paternal resources to her and their offspring (Buss, 1989; Ellis, 1992). In many cultures, these desires focus on cues to a man's status and prestige, his ambition and work ethic, his confidence and intelligence, his honesty and reputation for generosity, and his slightly older age (Buss, 2016; Cashdan, 1996; Kenrick & Keefe, 1992; Jonason et al., 2012; Li et al., 2020). In some cultures, a man's hunting ability, physical strength, body size, shoulder width, music ability, oratory skill, educational attainment, or other locally relevant armaments or adornments may be especially sought after in as much as they convey useful information about a man's ability and willingness to devote resources (Dixson, 2021; Frederick & Haselton, 2007; Gurven et al., 2009; Sell et al., 2017). Within foraging cultures, men's hunting abilities are particularly valued, with food provisioning via men's hunting contributing about 64 percent of the calories (Marlowe, 2001) and 85 percent of the protein (Kaplan et al., 2000) to the average forager diet. Foraging women particularly benefit from a husband's provisioning when they have young nurslings—a critical period during which women have lower foraging returns themselves while their husbands typically have higher returns (Marlowe, 2003b).

Women's food provisioning and general social status are also important for offspring survival (Hrdy, 2011), and under certain conditions men may prefer some of the exact same resource-related cues in women. For instance, cues to a woman's greater physical size, strength, and dominance may be especially preferred by men within cultures where women's ability to be physically tough and politically influential is tightly linked to familial resource acquisition (Cashdan, 2008; Fessler et al., 2012; Garfield & Hagen, 2020), by men who inhabit highly stressful ecological environments in which survival is especially difficult (Pazhoohi et al., 2021; Pollet & Nettle, 2008b; Sear & Marlowe, 2009), and by men whose sons need to be physically formidable in their local cultural context. Still, given the obligatorily higher levels of maternal compared to paternal investment required to rear human offspring successfully (Symons, 1979), evolutionary psychologists expect women, on average, will more strongly express long-term mate preferences for resource-related cues than men will in

most cultures around the world (Buss, 1989; Buss & Schmitt, 1993).

Sex Differences

Several lines of evidence have confirmed these expectations, including meta-analytical confirmation that women express preferences for long-term mating partners who exhibit resource-related cues (high social status, well-off family background, steady job, highly educated, high ambition/industriousness, good earning potential, good financial prospects, good economic prospects, relatively high earnings, relatively tall, wide shoulders, physically strong, masculine facial features, relatively older age) more than men do when asked in self-report surveys (Eastwick et al., 2014; Feingold, 1992). Sprecher et al. (1994) examined a nationally representative sample from the United States and found women, more than men, expressed long-term mate preferences for someone who had a *steady job* (d = -0.73), was *older* by five years (d = -0.67), *earned more* than they did (d = -0.49), and was *highly educated* (d = -0.43).[4] Most of these sex differences have remained relatively constant over historical time (Bech-Sørensen & Pollet, 2016; Buss et al., 2001; Chang et al., 2011; Gottschall et al., 2004; Kamble et al., 2014; Souza et al., 2016; cf. Zentner & Eagly, 2015).

Further supportive evidence of these sex differences comes from women's heightened responses to experimental manipulations of resource-related cues in potential mates (Marzoli et al., 2013; Strassberg & English, 2014) and from women's real-life choices of dating and marital partners (Egebark et al., 2021; Setinova & Topinková, 2021; Sidari et al., 2021). Wang et al. (2018), for instance, presented to participants from China, Lithuania, the United Kingdom, and the United States images of men's and women's body shapes along with information on their annual salary. Ratings of romantic attractiveness were around 1,000 times more sensitive to salary information when women rated men, compared to men rating women. In a large nationally representative sample of internet dating profiles in the United States, Anderson and Kolfstad (2012) found women engage in more resource-seeking than men do in real-life mate choice. In a field experiment in online dating, Ong and Wang (2015) found women of all income levels visit at higher rates men's profiles with higher incomes (e.g., profiles of men with the highest level of income received 10 times more visits than men with the lowest profiles), but men looking at profiles were largely unaffected by women's listed incomes. Importantly, these higher rates *increased* with the women's own incomes and even jumped discontinuously when the male profiles' incomes went above that of the women's own.

Evidence in support of women's evolved mate preferences also comes from

empirical linkages between men's resource-related traits and their fertility outcomes (Dunkel et al., 2019; Von Rueden et al., 2010). In comparing Czechian women's past sexual partners with the fathers of their children, Štěrbová et al. (2019) found Czechian fathers had more education, were taller, were more masculine (including masculine faces), and were more conscientious than ex-partner nonfathers. Nettle and Pollet (2008) documented that in the United Kingdom, a man's higher level of status is related to his higher fertility, but the same is much less true (or not at all true) for women's status. More widely, they noted selection gradients (links between cues to men's status and their fecundity or mating success) are generally even stronger when examined in preindustrial societies, such as the Hadza (β = .36), Aché (β = .31), and Tsimane (β = .22), compared to postindustrial societies, such as the United Kingdom (β = .10), the United States (β = .12), or Sweden (β = .17). Hopcroft (2021) recently demonstrated in a probability sample of the United States that higher-status men were more likely to marry than lower-status men. If divorced, higher-status men were more likely to remarry and were less likely to be childless than lower-status men. Most studies also find men who possess cues to high status are more likely to be married (especially remarried) to younger wives than are lower-status men (e.g., Kenrick & Keefe, 1992; Pollet et al., 2013).

Evidence in support of these hypothesized mate preferences also comes from evidence that expected sex differences are cross-culturally pervasive across non-WEIRD samples (i.e., non-Western, educated, industrialized, rich, and democratic samples; Apicella & Barrett, 2016; Thomas et al., 2020). Buss (1989), for instance, documented across 37 cultures that women, more than men, universally desire a slightly older long-term mate, whereas sex differences in preferences for "good financial prospects" were nearly universal (found in 97 percent of cultures), and sex differences in preferences for "ambition/industriousness" were prevalent (found in 78 percent of cultures). Several other large-scale investigations have replicated and extended these findings in non-WEIRD samples, documenting sex differences in resource-related mate preferences for good financial prospects, social status, ambition, and slightly or somewhat older age as pancultural universals across 100 percent of more than fifty studied nations (e.g., Lippa, 2007; Zhang et al., 2019). Most recently, Walter et al. (2021) found in a forty-five-nation sample (N = 14,399), culturally universal sex differences with women, more than men, preferring older mates and mates with good financial prospects in every sample studied.

Sex differences in many preferences for resource-related traits are also evident in ethnographic reports of preindustrial cultures (Smith & Apicella, 2020; cf. Sear & Marlowe, 2009). Among the Hadza hunter–gatherers of

Tanzania, Marlowe (2004) found most people ranked foraging ability highly in potential mates, but women ranked men's ability to provide food resources higher than men ranked women's foraging ability, noting that, "perhaps the most interesting result is that women placed more value on men being good foragers (85 percent of those women said 'good hunter') than on any other trait" (p. 374). Pillsworth (2008) documented among the Shuar—a modern hunter–horticulturalist population in Amazonian Ecuador—that among Shuar women, but not Shuar men, ratings of a peer target's "provider qualities" were significantly linked to ratings of desirability as a long-term romantic partner (women: $z = 3.05$, $p < .01$; men: $z = 0.92$, $p = .36$). Scelza and Prall (2018) observed among the Himba—a pastoralist society in northwestern Namibia in which men and women can take on both long-term and concurrent "informal" additional mates—that Himba women's mate preferences reflect a "men-as-investors" perspective, with women preferring both wealthy husbands and generous boyfriends. Himba women who have more dependents are especially likely to have strong preferences for wealthy and influential men as mating partners (Prall & Scelza, 2020). Finally, in a sweeping review of 33 preindustrial cultures, Von Rueden and Jaeggi (2016) found that men's status is consistently linked to higher reproductive success, regardless of how status was measured (e.g., physical formidability, hunting skill, material wealth, or political influence) and regardless of the culture's subsistence type (e.g., foraging, horticulture, pastoralism, or agriculture; see also Nettle & Pollet, 2008).

Individual Differences

In the case of mate preferences for resource-related cues, clearly not all women express equally strong preferences for a man who is both willing and able to devote resources (Buss & Barnes, 1986; Eastwick et al., 2006). A key contingency that may influence women's expression of these preferences may be her own personal circumstances (Kościński, 2011; Marcinkowska et al., 2021; Munro et al., 2014), including her personal access to resources. Evolutionary psychologists and others have tested whether women's preferences for mates who are able and willing to provide resources become sharply attenuated when women have ample resources of their own, as predicted by the *structural powerless hypothesis* (Buss & Barnes, 1986) and traditional *social role theory* (Eagly & Wood, 1999). Women might prefer cues to men's provisioning of resources, but only because women rationally make such decisions when structurally denied access to resources in their personal circumstance or culture.

Empirically, most studies have found that even when women possess very

high levels of resources themselves, they still prefer long-term mates who are able and willing to devote resources to themselves and their offspring (Anderson & Klofstad, 2012; Hughes & Aung, 2017). For instance, Fales et al. (2016) found in two nationally representative samples of the United States that among those individuals making *at least $95,000 a year*, 71 percent of women (but only 14 percent of men) *insisted* a potential long-term mate should have a steady income. Among those with advanced university degrees, 56 percent of women (but only 22 percent of men) considered it *very important* their mating partner made at least as much money as they did. In an online dating field experiment, Ong and Wang (2015) found that women of all income levels visit men's profiles with higher incomes at higher rates (while men were unaffected by women's listed incomes), and women's focus on high-income men *increased* with the women's own incomes and jumped discontinuously when the male profiles' incomes went above that of the women's own. It appears that personally possessing higher status and other resource-related traits does not fully attenuate individual women's expressed mate preferences for men's ability and willingness to provide resources. Instead, most evidence suggests that as women's personal status and resource levels go up, their insistence on men's ability and willingness to provide resources goes up as well.

Several other individual differences have been linked to women's mating strategies and mate preferences for resource-related cues in men (Lee et al., 2014; Penke et al., 2007). For instance, evidence suggests *high mate value* women—such as feminine women (Cunningham & Russell, 2004; Ellis & Ratnasingam, 2015) and physically attractive women (Feinberg et al., 2012; Little et al., 2001)—display the most marked long-term preferences for men with resource-related traits (see also Kavanagh et al., 2010). In a large cross-cultural study across 41 nations, women who rated themselves as more physically attractive consistently reported stronger preferences for exaggerated masculine, dominance-linked characteristics in men's faces (Marcinkowska et al., 2021b). Women who possess more masculine traits themselves (e.g., high childhood gender nonconformity or mental rotation ability) tend to pursue short-term mating strategies and emphasize physical attractiveness more than resource-related factors in potential partners (Clark, 2004; Mikach & Bailey, 1999). Women with traditional gender role ideologies tend to prefer men who are taller (Salska et al., 2008), are older, and possess good financial prospects (Eastwick et al., 2006).

Sensitivity to disgust reactions (e.g., Al-Shawaf et al., 2015, 2019a), political orientations (e.g., Koyama et al., 2004; Luberti et al., 2020), sexual orientation (Abé et al., 2021), personality traits (Lyons et al., 2015), and other individual

differences also appear to affect women's mating psychology in ways that influence preferences for resource-related traits. For example, women high in narcissism tend to emphasize "ambition/industriousness" and "good financial prospects" in potential long-term mates more than do women low in narcissism (Marcinkowska et al., 2021b). Postmenopausal women prefer men with more feminine faces compared to younger women (Jones et al., 2011), with preferences for masculine faces peaking among women at highest levels of fecundity (Little et al., 2010). Although heterosexual women generally prefer older men as long-term mates, even as they themselves age, older lesbians tend to prefer younger long-term partners compared to older heterosexual women (Kenrick et al., 1995). Lesbians tend to prefer more masculinity in female faces (and less masculinity in male faces) compared to heterosexual women (Shiramizu et al., 2020), though they are generally less discriminating about physical appearance (Bailey et al., 1997). Lesbians also place less emphasis than heterosexual women on a potential partner's social status (Bailey et al., 1994).

Increasing focus is being paid to how linear and nonlinear interactions between individual differences and mate preferences affect their expression in the real world (Clarkson et al., 2020; Conroy-Beam, 2018; Lee et al., 2014). More needs to be done to fully model the adaptive design of mate preference mechanisms, including how their impact comes online during development in some people but not others, uncovering which personality traits and mate preferences pattern together and why, working out which personal experiences and local circumstances accentuate some mate preferences while attenuating others, and determining how each mate preference has a particular biological and cultural evolution across space and time (Evans et al., 2021).

Cross-Cultural Differences

Cross-culturally, evolutionary psychologists have hypothesized that the expression of certain mate preferences, including those for resource-related cues, will vary around the world in ways that reveal adaptive design, including design features that impact the *size* of sex differences in expressed mate preferences (Buss & Barnes, 1986; Conroy-Beam et al., 2019; Schmitt, 2015). That is, evolutionary psychologists expect some psychological adaptations to generate behavioral variability in specially designed ways when exposed to certain environmental inputs such as critical developmental experiences (Ellis et al., 2009), aspects of current condition that might affect mate value (Harper et al., 2021), and other features of the local socioecology (e.g., sex ratios; Stone et al., 2007).

Several scholars have speculated that cultural and socioecological factors may play a role in *accentuating* women's heightened expression of preferences for resource-related cues, including the degree to which resources are important in a particular culture (e.g., resource acquisition and paternal investment may be more important in harsh socioecological contexts, especially for women who typically face higher costs in raising offspring; Cashdan, 2008; Low, 2005). Several studies have found support for this perspective. For instance, women prefer "good economic prospects" and "well-off family background" more strongly when in harsh socioecological contexts (Burtăverde & Ene, 2021; Moore & Cassidy, 2007). In a 30-nation study, DeBruine et al. (2010) found women prefer more ability-linked masculine faces in potential mating partners within nations that have worse health and life expectancy. Other studies, however, have found women may prefer men with more *willingness-linked* feminine faces when in especially harsh socioecologies (Little et al., 2007; Scott et al., 2014). Mixed results have also been found for cross-cultural effects of contexts where women have more or less personal control over resources (e.g., Fales et al., 2016).

Another reason sex differences in preferences for resource-related traits may be accentuated cross-culturally involves sex differences in socialization and women's levels of sociopolitical power within a culture (Buss & Barnes, 1986; Eagly & Wood, 1999). For instance, from a social role theory perspective, Eagly and Wood (1999) hypothesized women and men would report more similar desires for long-term mates who possess resource-related cues as a side effect of a culture's egalitarian sex role socialization and sociopolitical gender equality. They argue that "as societies become more egalitarian, men and women become more similarly positioned in the social structure and, therefore, more similar psychologically in many ways" (Eagly et al., 2004, pp. 283–284) and "this demise of many sex differences with increasing gender equality is a prediction of social role theory" (Eagly et al. 2004, p. 289).

Early tests of this social role perspective purported to find larger sex differences in the desire for long-term mates who possess resource-related cues in nations with less egalitarian sex role socialization and lower sociopolitical gender equality. Zentner and Mitura (2012), for instance, found sex differences in "ambition" shrink from a moderate effect size (d = -0.65) in lowest gender equality nations to a still moderate effect size (d = -0.48) in highest gender equality nations (see also Schmitt, 2016). Similar results were found for sex differences in desires for "social status" (d = -0.31) and "good financial prospects" (d = -0.55). Although these results are consistent with social role theory, the results do not suggest sex differences in resource-related mate

preferences are *eliminated* in high gender equality cultures (Stone et al., 2008).

Importantly, several recent studies have found *no links* between national gender equality and sex differences in mate preferences for resource-related cues (e.g., Walter et al., 2021), placing this social role explanation of women's mating desires in doubt. Zhang et al. (2019), for instance, found in a sample of 3,073 participants from 36 countries that although women preferred mates with "good earning capacity" more than men did, there was little evidence that these sex differences were smaller in countries with greater gender equality. One statistical association was found between sex differences in preferences for good earning capacity and greater sociopolitical gender equality, but this effect was eliminated when controlling for Galton's problem (Pollet et al., 2014) or correcting for multiple comparisons. Collectively, most recent studies have found little support for the notion that sociopolitical gender equality or personal access to resources impact women's long-term mate preferences for cues to men's ability and willingness to provide resources (Walter et al., 2021).

Overall, women more than men tend to place more emphasis on cues to the ability and willingness to provide resources (see table 4.1). In particular, women tend to value cues such as status and prestige, ambition and work ethic, confidence and intelligence, honesty and reputation for generosity, and slightly older age, and in some cultures, hunting ability, physical strength, body size, shoulder width, music ability, oratory skill, educational attainment, or other locally relevant armaments or adornments (Ellis, 1992). These preferences do not exist in all women from birth but rather emerge over time and are heightened in some women and in some socioecologies more than others. For instance, women who are especially feminine (Cunningham & Russell, 2004), are physically attractive (Buss & Shackelford, 2008), and possess resources themselves (Hughes & Aung, 2017) tend to value these cues more in potential long-term mates. Women also tend to pay more attention to these cues when in harsher socioecologies (Stone et al., 2008) and possibly when denied sociopolitical equality (Eagly & Wood, 1999; cf. Walter et al., 2021). Finally, individual and cultural circumstances appear to alter the relative importance of cues to men's *ability* to invest (i.e., masculinity; Cunningham et al., 1990; Lee et al., 2014) versus cues to his *willingness* to invest (i.e., nurturance; Little et al., 2007; Oh et al., 2020), leading women to engage in predictable trade-offs across cultures and socioecologies.

Thus, it is clear that to understand evolved mate preferences, it is pivotal to place them within proper cultural and socioecological contexts. As noted by Pisanski and Feinberg (2013):

Table 4.1 Sources of Variation in Expressed Mate Preferences for Cues to the *Ability* and *Willingness* to Devote Resources	
Sources of Variation	**References**
(1) Sex Differences: Women Prefer Cues More than Men	
• Surveys	Buss (1989); Eastwick et al. (2014); Waters et al., (2021)
• Experiments	Anderson & Kolfstad (2012); Egebark et al. (2021); Ong & Wang (2015)
• Fertility	Outcomes Hopcroft (2021); Nettle (2008); Von Rueden et al. (2010)
(2) Individual Differences of Mate Preferences within Women	
• Femininity: Feminine women value more than other women	Cunningham & Russell (2004); Ellis & Ratnasingam (2015)
• Attractiveness: Attractive women value more than other women	Buss & Shackelford (2008); Feinberg et al. (2012); Little et al. (2001)
• Traditionalism: Traditional women value more than other women	Eastwick et al. (2016); Salska et al. (2008)
• Orientation: Heterosexual women value more than lesbians	Bailey et al. (1994); Kenrick et al. (1995); Shiramizu et al. (2021)
• Resources: Women with own resources value more	Buss & Shackelford (2008); Hughes et al. (2017); Regan (1998)
3) Cultural and Socioecological Differences Particularly Affecting Women's Preferences	
• Women within harsh environments value more than other women	Burtăverde & Ene (2021); Moore & Cassidy (2007); Stone et al. (2008)
• Women within lower gender equity cultures value more	Eagly & Wood (1999); Zentner & Mitura (2012)
• Though several failures to replicate	Walter et al. (2021); Zhang et al. (2019)
(4) Tradeoffs and Additional Factors	
• Tradeoffs sometimes made between *ability* and *willingness*	Cunningham et al., 1998; Lee et al., 2014; Little et al, 2007; Oh et al., 2020

Note: Cues to the ability and willingness to devote resources include status and prestige, ambition and work ethic, confidence and intelligence, honesty and reputation for generosity, slightly older age; and in some cultures, hunting ability, physical strength, body size, shoulder width, music ability, oratory skill, educational attainment, or other locally-relevant armaments or adornments (Ellis, 1992).

> Evolutionary psychology provides a strong interdisciplinary framework from which to make context- and cost-dependent predictions about mating decisions. Cross-cultural research provides an ideal opportunity to test and construct evolutionary predictions about mating behavior across a number of highly heterogeneous contexts, wherein variation in geography, economy, communication, health, and family systems may prove essential to a comprehensive understanding of human mate preferences. (p. 184)

Trade-offs in Long-Term Mate Preferences

There are often multidimensional trade-offs that must be faced in mate choice (Cunningham et al., 2002; Oh et al., 2020; Schacht & Grote, 2015), such as women choosing between maximizing traits in men linked with the *ability* to

devote resources and their immunological competence (generally linked with dominance cues, such as high agency traits and more masculine faces and voices; Cunningham et al., 1990; Shiramizu et al., 2020) versus traits linked with *willingness* to devote resources and their paternal investment (generally linked with nurturance cues, such as interpersonal warmth and more feminine faces; Cunningham et al., 1998; Valentine et al., 2020). Perhaps as a result, evidence of women's long-term heightened preferences for "masculine" or more male-typical faces and bodies is somewhat mixed (Clarkson et al., 2020; Marcinkowska et al., 2019; Stower et al., 2020).

Some studies find women pursuing short-term mates tend to express heightened desires for masculine faces and formidable bodies (DeBruine et al., 2006; Sacco et al., 2012), as do women who experience earlier menarche and engage in more mating effort than parenting effort (Niu & Zheng, 2020), and women who reside within cultures where engaging in short-term mating is more common (Marcinkowska et al., 2019). Women who are fearful of crime and view themselves as potentially benefiting from protection prefer masculine partners as long-term mates (Snyder et al., 2011), and women who perceive themselves to have low personal control (e.g., "Many things in my life are beyond my influence") tend to prefer mating partners who possess cues to high status (e.g., "Has high status" and "Has good financial prospects"; Lammers & Inhoff, 2021).

Masculinity-seeking women appear to preferentially prioritize cues to *ability*-related traits in their mate preferences, traits linked with an increased capacity for men to procure resources in local environments. Such traits also may be linked to so-called good genes traits that are indicative of superior immune system (Rantala et al., 2012), disease resistant (Thornhill & Gangestad, 2006), and subsequently fitness-enhancing for women's sons (Kruger, 2006; Oh et al., 2020). The dual mating strategy hypothesis specifically proposes that women especially select more masculine partners when the costs of reduced paternal investment are minimized and the possible genetic benefits to future offspring are maximized (Gangestad & Simpson, 2000; Muggleton & Fincher, 2017).

Ability-related masculinity in men may also be linked to cultural levels of aggression and violence. If so, women may trade off nurturing willingness cues for dominating ability cues when in high stress and violent cultural contexts (Snyder et al., 2011). In some cultures, "high levels of direct physical competition and violence among males may increase the importance of direct intra-sexual competition" and in those cultures, "it may be adaptive for women to shift visual preferences in favor of males with face cues indicating physical strength and dominance over investment in such environments" (Little, 2013, p.

193). High masculinity also may be associated with men's tendencies to pursue short-term mating strategies (Boothroyd et al., 2008) which may jeopardize long-term relationship stability. These risks appear worth the trade-off for women in certain personal and socioecological contexts (McGraw, 2002), but not others (Borras-Guevara et al., 2017). For instance, women who report low status themselves tend to prefer more feminine male faces, perhaps as this is linked with men's *willingness* to invest in long-term mateships and to good parenting ability (Lee et al., 2014; Little et al., 2007). Little et al. (2001) suggested that the relatively decreased preference for masculinity among women who regard themselves as unattractive may represent a facultative mating strategy, with women of low mate value avoiding the costs of decreased parental investment when mating with men who possess masculine markers of good genes.

Men's Long-Term Mate Preferences

Evolutionary psychologists have hypothesized that men may have evolved mate preferences for cues that reliably signal a woman's fecundity (i.e., the ability to produce an abundance of offspring), including cues to her relative youth and health (Buss, 1989; Cloud & Perilloux, 2014; Cunningham, 1986; Symons, 1979). Such cues may reflect both her current fertility status (i.e., odds of conceiving at the moment) and her potential long-term reproductive value (i.e., number of children a woman could have into the future; Buss & Schmitt, 1993). In short-term mating, men tend to especially emphasize cues to current fertility status (see Buunk et al., 2001; Symons, 1995). However, in long-term mating, issues of compatibility and retention also become central to forming an enduring pair-bond (Buss & Schmitt, 1993; Penke et al., 2007; cf. Sohn, 2017).

In general, the specific physical features indicative of a woman's youth and relatively high fecundity include possessing a neotenous face (i.e., full lips, wide eyes, and relatively small jaw and chin), lustrous hair, clear and glowing skin, good muscle tone, and a low waist-to-hip ratio (estimated around 0.7) which is indicative of optimal body fat distribution (Cunningham et al., 1995; Stephen & Luoto, forthcoming; Sugiyama, 2015). These indicators reliably signal a woman's age and also some aspects of her health (Rhodes, 2006; Voegeli et al., 2021), maternal tendencies (Smith et al., 2012), and the ability to provide neurodevelopmental resources for offspring during gestation (Lassek & Gaulin, 2008). Some of these cues may also be especially informative of women's nulliparity (i.e., having reached reproductive maturity but not yet having had children; Lassek & Gaulin, 2019; Symons, 1995). However, some of these cues

are reliably indicators only of youth and therefore levels of fecundity only relative to women of all ages (not relative to women of the same age; Bovet, 2019; Jones et al., 2022).

Two prominent theories of human mating predict that women pay attention to men's health and genetic quality as well (especially in short-term mating; Buss & Schmitt, 1993; Gangestad & Simpson, 2000). However, within women these desires take somewhat different forms such as preferences for cues to masculine facial structure (e.g., strong brow and large jaw and chin), broad shoulders, physical strength, tall height, high shoulder-to-waist (or hips) ratios, a 0.9 waist-to-hip ratio of body fat distribution, and deep voice pitches (see Ellis, 1992; Lidborg et al., 2020; Sugiyama, 2015). Some of these masculine features in men appear to be linked with better health and fertility outcomes (Reyes-Garcia et al., 2008; Sell et al., 2009). Still, even though both men and women prefer certain cues related to physical appearance, the precise cues that convey relevant adaptive information, are attended to most keenly, and are thought of as "physically attractive" are somewhat sex-differentiated. Crucially, the relative import of physical attractiveness cues *when long-term mating* is hypothesized to be higher, on average, in men than women (Buss & Schmitt, 1993; Symons 1979).

Sex Differences

Several lines of evidence have confirmed hypotheses that men possess preferences for physical attractiveness cues that reliably signal a woman's fecundity and relative youth (e.g., Buss, 1989; Lippa, 2007). Feingold (1990) conducted a meta-analysis of mate preferences and confirmed men prefer indicators of "physical attractiveness" in potential long-term mates more than women do (overall d = 0.54). Numerous studies since have replicated sex differences in long-term mate preferences for physical attractiveness, especially cues to youth (Conroy-Beam & Buss, 2019). Sprecher et al. (1994), for instance, in a representative sample from the United States found men, more than women, especially value "good looks" (d = 0.65) and "younger age" (d = 0.99). Schwarz and Hassebrauck (2012) surveyed 21,245 single people between eighteen and sixty-five (average age = 31) and found men valued physical attractiveness and relative youth more than women, regardless of age or education level. Men's specialized emphasis on particular youth and fecundity-linked attractiveness cues is even found among the blind (Karremans et al., 2010; Scheller et al., 2021).

Some real-world tests of men's actual mating experiences and mate choices

have confirmed cues to fecundity and youth influence face-to-face evaluations of attractiveness by men (Li et al., 2013; Roth et al., 2021; Sidari et al., 2021). Many of men's courtship and interpersonal interactions with women appear affected by these preferences. Experimentally, men exposed to physically attractive women react by valuing money, experiencing greater ambition, being more creative, and being willing to take more risks (Roney, 2003). Men told they were making a phone call to a woman lowered their voice (a feature women typically find attractive), but only if the woman was portrayed as highly physically attractive (Hughes et al., 2010). Cues to fecundity and youth seem to matter profoundly to men, and these evolved mate preferences impact their stated desires, their courtship behaviors, and their actual real-world mate choices (Buss & Schmitt, 2019).

Individual Differences

Clearly not all men express equally strong mate preferences for women who possess cues to relative youth and fecundity. Though relatively few in number, some men are gerontophilic and find elderly women the most erotically interesting (Seto, 2017), whereas others are particularly attracted to women who are currently pregnant or lactating (Enquist et al., 2011). Although men's feelings of erotic attraction are flexible and show some evidence of sexual imprinting (Bereczkei et al., 2004), evolutionary psychologists expect most men will find women who possess cues to the ability to have children now and into the future (i.e., possess high reproductive value) to be the most attractive as potential long-term mates (Buss, 1989; Conroy-Beam & Buss, 2019).

Evolutionary psychologists have also hypothesized that some men may be especially likely to prefer cues to relative youth and fecundity. For instance, men with *high mate value* (e.g., men who possess resource-related cues) may be the most likely to exhibit strong preferences for cues to women's youth and fecundity. Such men may be better able to attract and retain women who possess high mate value themselves. Such men may also be expected to expend more energy on mating efforts compared to parenting efforts (Burnham et al., 2003; Gettler et al., 2011). Among the Hadza, a foraging society in Tanzania, Marlowe (1999) documented that men provide less care to their biological children and focus on mating effort as their status-related opportunities increase. Men's mate preferences for youth and fecundity may be more activated and influential in courtship behavior and mate choice among higher status men than lower status men (Gangestad & Simpson, 2000).

Evidence in support of high mate value men preferring cues to youth and

fecundity more than low mate value men is substantial. In representative samples from the United States, Fales et al. (2016) found wealthier men, but not wealthier women, had stronger preferences for good-looking partners. Heath and Hadley (1998) reported that wealthy men tend to invest their wealth in mating effort by channeling resources toward other potential mates. However, poor men with meager resources tend to invest what resources they have in parental effort (Marlowe, 1999). Little et al. (2014) found men who consider themselves more physically attractive (e.g., possess masculine faces) tend to prefer women who have more feminine faces as potential mates, especially as short-term partners (see also Burris et al. 2011; Price et al., 2013). This appears to be especially true in low stress and low violence cultural contexts (Marcinkowska et al., 2021b), within which men's preferences for femininity in women are generally heightened (Cashdan, 2008).

Other individual differences that may influence men's preferences for cues to relative youth and fecundity include age, masculinity, and possibly testosterone levels (Buunk et al., 2001; Conroy-Beam & Buss, 2019). In general, more masculine men and men whose age is typically linked with higher testosterone tend to value cues to youth and fecundity more in their potential mating partners (Little et al., 2011; Welling et al., 2008). For instance, men's preference for women with especially feminine faces peaks in men in their thirties and declines thereafter, as men's testosterone levels fall (Marcinkowska et al., 2017). Men who marry tend to experience a drop in their testosterone, unless they are seeking extramarital affairs (McIntyre et al., 2006). Han et al. (2020) found experimentally that a single dose of 150 mg testosterone (vs. a placebo) increased men's attraction to women with especially feminine faces. Welling et al. (2013) used experimental methods to document that men unknowingly assigned to be winners of a videogame competition showed an increased preference for facial femininity relative to randomly assigned competition losers. Men's political attitudes (e.g., endorsement of feminism) appear unrelated to their mate preferences for youth and fecundity-related cues (Koyama et al., 2004). Shiramizu et al. (2020) found gay men showed significantly weaker preferences for feminized female faces (but stronger preferences for masculine male faces) than do heterosexual men.

Cross-Cultural Differences

Cross-culturally, evolutionary psychologists have hypothesized that preferences for cues to youth and fecundity will be expressed more strongly in men than in women in most cultures. This hypothesis has been strongly

confirmed in several studies. Buss (1989) surveyed long-term mate preferences across 37 cultures and found men prefer younger women as long-term mates in 100 percent of cultures, and men preferred "good looks" in potential long-term mates more than women did across thirty-four of thirty-seven cultures (92 percent). In no cultures did women prefer physical attractiveness significantly more than men did in long-term mates. These results were replicated in a larger cross-cultural study by Lippa (2007) who found sex differences in "good looks" mate preferences across 100 percent of fifty-three cultures, with an average effect size of $d = 0.55$. Similar results have been reported by Zhang et al. (2019) across thirty-six nations. An independent team of researchers has replicated these findings across forty-five nations (Walter et al., 2021). Zentner and Mitura (2012) found sex differences in mate preferences for good looks were a pancultural universal across 100 percent of ten nations, and that sex differences were larger as sociopolitical gender equality increased across nations, directly contrary to predictions from social role theory. Zentner and Mitura (2012) found low sociopolitical gender equality nations displayed smaller sex differences ($d = 0.24$) compared to medium ($d = 0.43$) or high sociopolitical gender equality nations ($d = 0.51$). This finding suggests increased sociopolitical gender equality in a nation does not reduce the size of sex differences in mate preferences for physical attractiveness. If anything, it increases it (see also Schmitt, 2015).

Evolutionary psychologists have outlined several reasons for expecting men's (and women's) mate preferences for physical attractiveness to shift across cultures. One important factor is pathogen loads in the local ecology (Schaller & Murray, 2008; Sng et al., 2018; cf. Dixson et al., 2017). Gangestad and Buss (1993) were among the first to demonstrate that women's and men's mate preferences for physical attractiveness are closely linked to local pathogen levels, with good looks being more important in high pathogen socioecologies, even after controlling for income, geographical region, and latitude (Gangestad et al., 2006; see also Little et al., 2007; Quinlan, 2007; cf Walter et al., 2021). Cantú (2013) found women are especially affected by pathogens in their preferences for physical attractiveness. For instance, across two experiments she found that when pathogen prevalence was temporarily salient, women (but not men) exhibited an exaggerated preference for physically attractive mates. If women's mate preferences for physical attractiveness are more reactive to local pathogen levels, this may explain why sex differences in preferences for physical attractiveness are smaller in high pathogen cultures (Low, 1990; Schmitt, 2014).

Other cultural and socioecological factors have been shown to affect men's mate preferences for youth and fecundity. For example, according to the economic security hypothesis (Pettijohn & Jungeberg, 2004), men's preferences

for youth and fecundity may be especially evident when the local culture and socioecology are relatively safe, secure, and healthy. Indeed, several studies have found men prefer more feminine women in times of economic security and low mortality. For instance, Marcinkowska et al. (2014) found across twenty-eight nations that men's facial femininity preferences were positively associated with higher health of a nation. The highest preferences for feminine faces were exhibited by Japanese men, whereas the weakest preferences for femininity were found in Nepalese men. Overall, national health explained 50.4 percent of the variation in men's facial femininity preferences. Marcinkowska et al. (2014) speculated that in less safe and healthy environments, men prefer cues that would be linked to women's dominance and foraging skills rather than to their youth and high fecundity. Previous studies in Bangladesh (de Barra et al., 2013) and Jamaica (Penton-Voak et al., 2004) have also found that men in less safe and healthy environments exhibit much weaker preferences for cues to youth and fecundity.

Overall, most research confirms that men more than women tend to value cues to youth and fecundity in potential long-term mates (see table 4.2). In particular, men more than women tend to desire mates who possess cues such as facial neoteny (e.g., full lips, wide eyes, and relatively small jaw and chin) and a 0.7 waist-to-hip ratio of body fat distribution (Stephen & Luoto, forthcoming; Sugiyama, 2015). These preferences do not exist in all men from birth but rather emerge across development (e.g., partly via organizational or activational effects of hormones; Schmitt, 2017) and are heightened in some types of men and in some types of cultures and socioecologies more than others. For instance, men who are particularly masculine, who are wealthy, or who possess higher testosterone express stronger preferences for youthful and highly fecund women. Findings across cultures are more mixed. Several studies have found men and women express stronger preferences for physical attractiveness within high pathogen environments (Gangestad et al., 2006), and some have found women's reactions to pathogens are stronger (Cantú, 2013; Luoto & Varella, 2021) leading to sex differences in physical attractiveness preferences being smaller in high pathogen cultures (Schmitt, 2014). However, other studies have found men's preferences for physical attractiveness are reduced in less safe and healthy cultures (Marcinkowska et al., 2014).

Table 4.2 Sources of Variation in Expressed Mate Preferences for Cues to the Women's *Youth* and *Fecundity*

Sources of Variation	**References**
(1) Sex Differences: Men Prefer Cues More than Women	

• Surveys	Buss (1990); Feingold (1990); Kenrick et al. (1990); Lippa (2007)
• Experiments	Lynn (2009); Puts (2005); Stirrat (2011); Yong (2012)
• Real-world mate choice	Li et al. (2013); Sidari et al. (2021)
(2) Individual Differences of Mate Preferences within Men	
• Masculinity: Masculine men value more than other men	Burris et al. (2011); Little et al. (2014); Price et al. (2013)
• Wealth: Wealthy men value more than other men	Buss (2000); Fales et al. (2015); Hadley et al. (1998)
• Testosterone: High testosterone men value more than other men	Han et al. (2020); Marcinkowska et al (2017); Welling et al. (2008)
(3) Cultural and Socioecological Differences Affecting Men's (and Women's) Preferences	
• Men within high pathogen cultures value more than others	Gangestad & Buss (1993); Gangestad et al. (2006)
• Women more reactive, leads to smaller sex differences	Cantu (2013); Low (1990); Schmitt (2014)
• Men within less safe and healthy cultures value less than others	Marcinkowska et al. (2014); Pettijohn & Jungeberg (2004)

Note: Cues to the women's youth and fecundity include possessing a neotenous face (i.e., feminine face consisting of full lips, wide eyes, relatively small jaw and chin), lustrous hair, clear and glowing skin, good muscle tone, and a 0.7 waist-to-hip ratio of body fat distribution (Stephen & Luoto, 2021; Sugiyama, 2015; Thornhill & Gangestad, 1999).

Future research will need to more clearly outline which specific cues of women's physical attractiveness (e.g., full lips, wide eyes, relatively small jaw and chin, a 0.7 waist-to-hip ratio, and optimal lumbar curvature) men value more across differing conditions of environmental stress (e.g., high pathogens, high mortality, low safety, low general health, and skewed sex ratios). It is likely there are special design features across different mate preference mechanisms (i.e., sensitivities to some inputs more than others) that will lead to their expression being heightened under differing socioecological conditions (Schaller & Murray, 2008; Sng et al., 2018). Moreover, the full expression of mate preferences may emerge in dynamic interaction with other context-sensitive psychological adaptations (e.g., behavioral immune system; Luoto, 2019; Schaller, 2016), and there may be ontogenetic critical periods in men during which some mate preferences are more likely to be turned on or enhanced (e.g., by in utero or pubertal exposure to testosterone; Luoto et al., 2019; Schmitt, 2017).

Key Socioecological Triggers of Human Mating Strategy Variation

Human behavioral ecologists, evolutionary anthropologists, and evolutionary

psychologists have documented a wide range of cultural and socioecological factors that seem to reliably trigger shifts in human mating psychology (Gangestad et al., 2006; Low, 2007). Factors such as socioecological harshness, inheritance rules, and postmarital residence traditions have been linked to culturally evoked patterns of marital infidelity (Hartung, 1985), premarital sex (Barber, 2001), jealousy (Scelza et al., 2020a), romantic love (Schmitt et al., 2009), and gendered social networks (Mattison et al., 2021). Sng et al. (2018) recently highlighted the special importance of six socioecological factors that seem to especially impact the development and activation of evolved psychological adaptations: (1) *population density* (e.g., higher density is generally linked to slower life history traits and less competitiveness and aggression; Rotella et al., 2021; Sng et al., 2017), (2) *genetic relatedness* (e.g., higher relatedness is generally linked to more alloparenting and prosociality), (3) *mortality rates* (e.g., higher mortality is generally linked to faster life history traits), (4) *resource availability and predictability* (e.g., lower availability and predictability is generally linked to decreased reproduction and increased risky behavior), (5) *disease and pathogen prevalence* (e.g., low pathogen levels are generally linked to slower life history traits and more emphasis on resources), and (f) *operational sex ratios* (e.g., the more common sex tends to face greater sexual selection pressures such as intrasexual competition). Two of these socioecological factors have been closely linked with mating psychology shifts across cultures: pathogen levels and sex ratios.

Pathogens

Pathogens have been implicated as a key socioecological trigger that affects human mating psychology, often in connection with the prevalence of polygynous mating in a culture. Polygyny, in which some men are able to have more than one wife, is the most common social mating system in preindustrial human cultures (Marlowe, 2003a). In the Standard Cross-Cultural Sample (SCCS), 83.8 percent of societies are socially polygynous; with 28 percent coded as have more than 40 percent of marriages being polygynous (Marlowe, 2003a). Moreover, presumptively “monogamous” human cultures often function as biologically polygynous due to sex differences in rates of infidelity and in men’s greater likelihood of achieving polygyny via serial monogamy (through men’s greater likelihood of remarriage and continued fertility after divorce; see Hopcroft, 2021; Miller et al., 2021; see also Mulder, 2009). The type and intensity of polygyny varies across human cultures. Among the Aché of Paraguay only about 4 percent of men have multiple wives, but this rate is 6

percent among !Kung San of Namibia, 23 percent among the Warao of Venezuela, 36 percent among the Batek of Southeast Asia, and 47 percent among the Alywara of Australia (see Hill & Hurtado, 1996). This variability in degree of human polygyny may stem from evolved psychological adaptations reacting to local socioecological conditions such as pathogen stress (Marlowe, 2003a; Yanca & Low, 2005).

Low (1990) was among the first to document that cultures with high pathogen stress are more likely to have polygynous marriage systems. Across samples from the 186 societies of the SCCS (Murdock & White, 1969), Low found the degree to which men and women were in polygynous marriages was positively linked to high levels of pathogens in the local ecology, including malaria, leprosy, and spirochetes. Schmitt and Rohde (2013) found pathogen levels were strongly linked to the degree of polygynous mating behavior across forty-eight economically complex nations of the International Sexuality Description Project. These links may be explained, in part, from high-pathogen ecologies evoking in men stronger preferences for genetic diversity in their offspring (or other mating desires that would function to achieve polygyny), while women may especially prefer healthy men who can support multiple wives in high pathogen contexts—a pattern also related to the *polygyny threshold model* (Mulder, 1988; Weatherhead & Robertson, 1979; see also Ross et al., 2018). Mating adaptations designed to respond to pathogen levels may also give rise to different forms of polygyny. For example, in environments with high pathogen levels, polygynous men tend to marry exogamously, outside their local group, which further increases their offspring diversity. Sororal polygyny, men marrying women who are sisters, provides less genetic diversity and rarely occurs in environments with high pathogen levels (Low, 2000).

In a review of socioecological links to human polygyny intensity, Ember et al. (2007) found the two biggest predictors of polygyny were high male mortality in war (resulting in a female-biased sex ratio) and high pathogen stress (polygyny functioning to maximize genetic variation and disease resistance in progeny; see also Marlowe, 2003a). Other culture-level correlates of polygynous mating systems in humans include several factors related to pathogen loads, including climate (polygyny is more prevalent in tropical and temperate zones), general food security (polygyny is more prevalent in less food secure cultures), poor child health (polygyny is more prevalent in cultures with more child illness), bride wealth and patrilocality (polygyny is more prevalent where a woman's family is provided payment before marriage and women move to live with their new husband's family), warfare capture of women (polygyny is more prevalent where men frequently plunder other groups and marry captured women), and

women's food provisioning (polygyny is more prevalent where women contribute more to the diet; White & Burton, 1988; Marlowe, 2003b). Some of these links may depend on how polygynous mating is defined (White, 1988) and further hinge on whether the links are examined at cultural or individual levels (e.g., poor food security and child illness; Lawson et al., 2015).

Schaller and Murray (2008) have speculated that pathogen loads affect people's pursuit of long-term versus short-term mating strategies (i.e., sociosexuality). They reasoned that the fitness costs associated with short-term mating with lots of partners (e.g., infection or disease) must be weighed against fitness benefits (e.g., among men, short-term mating strategies may confer benefits through the production of more offspring; among women, short-term mating may confer benefits of genetically diverse offspring or genetically superior offspring relative to her husband). These cost/benefit ratios are likely to vary depending upon the prevalence of pathogens in the immediate ecology. In environments where the prevalence of pathogens is high, the costs of short-term mating may be more likely to outweigh the benefits (Tybur et al., 2012). Thus, in ecologies that have a high prevalence of pathogens, some evolutionary psychologists expect, and typically find, more "long-term orientated" mating strategies (Thornhill et al., 2010; cf Bromham et al., 2018). Similarly, high pathogen levels are linked with heightened religiosity (Fincher & Thornhill, 2008) and authoritarianism (Murray et al., 2013), both of which may be evoked psychologies in ways that reduce people's risk for socially linked infections and diseases.

Pathogen levels and other indicators of environmental harshness have been suggested to affect several other features of human mating psychology (Quinlan, 2007). As noted earlier, pathogen prevalence appears to shift people's emphasis on physical attractiveness in potential mates, possibly heightening women's emphasis on men's possession of cues to genetic quality and immunocompetence (Gangestad et al., 2006). De Barra et al (2013 found indicators of high pathogen levels (e.g., childhood illness and frequency of diarrhea) are positively linked with preferences for exaggerated sex-typical characteristics in opposite-sex faces (e.g., women's emphasis on men's facial masculinity) but not same-sex faces. Moreover, this relationship appeared to be stronger among individuals with poorer current health. Little et al. (2007) hypothesized that facial symmetry may be preferred more in regions where pathogen load is high and levels of immunocompetence are more important (e.g., East Africa; Low, 1990). Whereas both UK and Tanzanian populations preferred symmetrical to asymmetrical opposite-sex faces, preferences for symmetry were strongest among Tanzanian Hadza hunter–gatherers. This was especially true among Hadza men who were

named as “good hunters” by others (Little et al., 2007), confirming earlier accounts that men with high mate value are more likely to prefer cues to physical attractiveness in potential mates.

Scelza et al. (2021) documented among the Himba pastoralists of northwest Namibia that in their relatively harsh socioecology, the costs of Himba men’s mate guarding and the benefits of producing genetically robust offspring may be sufficiently high to produce a mixed form of nonmonogamous mating. Himba women and men have both formal marital partners and informal (but still long-term) mating partners, with 48 percent of children resulting from extra-pair paternity (the biological father is not the mother’s husband) and 70 percent of couples having at least one extra-pair paternity child (Scelza et al., 2020b). This “concurrent” mating system coincides with cultural values and institutions that provide women relatively high reproductive freedom (e.g., ease of divorce, partner choice in second marriages, low stigmatization of out-of-wedlock births, and an extensive fosterage system that allows women to leave their existing children with their mothers when a new marriage is formed; Scelza et al., 2021).

Table 4.3 Variation in Mating Psychology across Socioecological Conditions around the World

Socioecological Conditions and Mating Psychology	**References**
(1) *Higher Levels of Pathogens*	
• Higher levels of polygynous mating	Low (1990, 2000); Schmitt & Rohde (2013)
• Lower levels of sociosexuality (i.e., less short-term mating)	Thornhill et al. (2010); Schaller & Murray (2008)
• Personality traits associated with less intergroup mating	Schaller & Murray (2008)
• Stronger mate preferences for sex-typical traits	DeBarra et al. (2014); DeBruine et al. (2010)
• Stronger mate preferences for physical attractiveness	Gangestad et al. (2006); Lee & Zeitsch (2011); Little et al. (2007)
• Faster life history traits (e.g., higher fertility, less parental investment)	Guégan et al. (2001); Hill et al. (2016); Luoto (2019); Quinlan (2007)
(2) *Higher Operational Sex Ratios* (i.e., more men than women in local mating pool)	
• Lower levels of polygynous mating	Pollet & Nettle (2009)
• Higher levels of polyandrous mating	Starkweather & Hames (2012)
• Lower levels of sociosexuality (i.e., less short-term mating)	Moss & Maner (2016); Schmitt (2005)
• Lower divorce rates	Blurton-Jones et al. (2000)
• Higher levels of paternal investment in offspring	Marlowe (1999)
• Higher levels of men displaying masculinity and cues to resources	Barber (2001); Griskevicius et al. (2012)
• Higher indicators of intrasexual violence and risk-taking among men	Ackerman et al. (2016); Barber (2003)
• Lower levels of women seeking resources	Durante et al. (2012)

themselves	

Operational Sex Ratios

Operational sex ratio (OSR) is the ratio of reproductive-age males to reproductive-age females in a given mating pool. Typically, human OSRs are considered "high" when populations contain more reproductive-age men than women, and "low" when there are more reproductive-age women than men (Moss & Maner, 2016; Pedersen, 1991). Because OSRs influence the availability of potential mates, strongly unbalanced OSRs may affect sexual selection pressures by heightening the intensity of intrasexual *competition* within the sex that is more numerous while heightening the intensity of intersexual *selection* within the sex that is rarer (Guttentag & Secord, 1983; Trivers, 1972). When there are many more men than women, for example, the plentiful men may have to intrasexually compete more forcefully against one another to effectively provide highly selective women with what they desire (Stone et al., 2007; Walter et al., 2021).

In humans, women generally desire higher levels of commitment before consenting to sex than men do (Schmitt, 2005). As a result, evolutionary psychologists expect, and have found, higher OSR contexts (within which women are rarer and can thereby command more in the mating marketplace) are associated with increases in indicators of long-term mating and sociosexually "restricted" orientations (Arnocky et al., 2016; Pedersen, 1991; Schmitt, 2005). For instance, observed shifts across historical time have demonstrated higher OSRs (more men than women) coincide with higher marriage rates, lower divorce rates, fewer illegitimate births, fewer teen births, and higher paternal investment (Kruger, 2009; Pollet & Nettle, 2008a). Across 2,800 counties in the 2010 US Census, Schacht and Kramer (2016) found high OSRs in a county were associated with men being more likely to marry, to currently be part of a family, and to be sexually committed to a single partner.

Higher OSRs are also cross-culturally associated with long-term mating and restricted sociosexuality in men and women (Kandrik et al., 2015; Schmitt, 2005). Again, this may be due to women being rarer and so they are better able to command the mating marketplace and impose their greater interest in high-commitment mating (Pedersen, 1991). Higher OSRs have been associated across cultures with both lower levels of polygynous mating (Pollet & Nettle, 2009) and higher rates of polyandry (Starkweather & Hames, 2012), again perhaps reflecting women's command of the mating marketplace as the rarer sex. High OSRs across cultures also are associated with more relaxed long-term mate preferences by men, possibly in order to facilitate the acquisition of the less

numerous and highly selective women partners (Stone et al., 2007). Experimentally manipulating impressions of OSRs by making men appear more common than women is associated with more long-term mating and restricted sociosexuality (Moss & Maner, 2016). When men are rarer than women (i.e., low OSRs), men are better able to sway the mating marketplace, and low OSRs are historically, cross-culturally, and experimentally associated with several increases in indexes of short-term mating (Pedersen, 1991; Schacht & Borgerhoff Mulder, 2015).

Further support for the view that human mating psychology is designed to strategically shift in response to OSR variation comes from studies of intrasexual competitiveness and direct mating effort (Arnocky et al., 2014; cf. Schacht et al., 2014). Higher OSRs are historically and cross-culturally associated with higher levels of men's intrasexual aggression and violence (Barber, 2000, 2003; Hudson & Den Boer, 2002). Across 120 cities in the United States, higher OSRs were associated with indexes of men's impulsiveness, such as owning more credit cards and having a higher amount of debt on the credit cards they do have (Griskevicius et al., 2012). Experimentally, higher OSRs are linked to men focusing on immediate rewards, rather than saving for the future, and appear to lead men to spend more money during courtship (e.g., paying more for engagement rings, Griskevicius et al., 2012). Higher OSRs seem to evoke tendencies in men to diversify financial resources less and instead concentrate investment in high-risk/high-return options when making lottery, stock-pool, retirement-account, and research-funding decisions (Ackerman et al., 2016).

There is evidence that women also adjust their mating efforts in response to shifts in OSRs (Dillon et al., 2015; Wang et al., 2020). For instance, Arnocky et al. (2014) experimentally manipulated perceived OSRs and found women exposed to a low OSR mating market with a scarcity of men reported more intrasexual competition, jealousy, and willingness to aggress indirectly against a mate poacher compared to those exposed to an abundance of males. Durante et al. (2012) demonstrated across historical data and experimental manipulations that lower OSRs are associated with women (especially low mate value women) seeking high-paying careers and delaying the start of their families. In contrast, women in higher OSR nations tend to marry early as a reflection of a more restricted sociosexuality (Trent & South, 2011). Given the extant evidence from cross-cultural, historical, and experimental studies, variations in operational sex ratios appear to be associated with changes in human mating behavior, including predictable features of sociosexuality, intrasexual mate competition, and intersexual mate choice (Walter et al., 2021).

Future Research Directions

This chapter focused mainly on evolutionary psychological approaches to understanding human mating across cultures, especially facultative adaptations and evoked culture concepts (Gangestad et al., 2006; Sng et al., 2018; Tooby & Cosmides, 1992). Other approaches within the evolutionary behavioral sciences have shed considerable light on human mating practices around the world, incorporating new findings and techniques across disciplines such as human behavioral ecology, evolutionary anthropology, and cultural evolution (Brown & Richerson, 2014; Luoto, 2019). A truly complete understanding of human mating psychology and its expression across cultures will require the combined insights of all these approaches. Indeed, many evolutionary behavioral scientists focusing on human mating no longer utilize techniques from just a single scholarly discipline; rather, they utilize whatever are the best methods for answering the types of questions they are currently asking. Over the last decade, the integration of what were once separate approaches to evolutionary behavioral science is being achieved (Brown & Richerson, 2014).

Evolutionary behavioral sciences could benefit from extending their expertise even further into historical, economic, and sociological contextualizations of human mating psychology and its cultural manifestations (Turner & Machalek, 2018). For instance, when seeking to fully understand mate preferences not within a broad culture but within a particular social group of humans, Fuentes (2016) suggested that many different perspectives are required. Scholars need to consider that sexual selection has influenced the morphologies, behaviors, and sexual processes of observed mate choice. Scholars need to observe people's real-world patterns of mate choice, consider individual variation in mate choice, take into consideration the many mismatches between our evolved mating psychology and the current mating environments (Goetz et al., 2019), and examine how local ecological contexts affect sex differences and individual differences. Many of these features have been addressed in this chapter. But more is needed for a complete understanding of mate preferences. Scholars also need to model the structural constraints and facilitators provided by specific reproductive physiology in humans, more fully incorporate aspects of group and community demography, and examine how individual and group perceptions of gender roles across history affect mate choice.

This chapter was limited primarily to reviewing aspects of mate choice within long-term mating contexts. New and emerging evidence suggests that people's mate preferences may vary across several relationship contexts, contexts that extend well-beyond the simple short-term/long-term categorizations (Scelza &

Prall, 2018) and individualistic mate choices (Apostolou, 2017; Brooks & Blake, 2021) that typify work in the field. Different cues may give adaptive information relevant to some mating contexts more than others (Cloud & Perilloux, 2014; Hill et al., 2013; Seffrin & Ingulli, 2021). It may be that the effects of sex, personal circumstance, and socioecology on mate preferences reviewed here vary in important ways across diverse forms of mateships, including contexts such as mate poaching, infidelity, concurrent mating, and consensual nonmonogamy (Mogilski et al., 2017). Future work should also focus on the variable developmental emergence (Larsen et al., 2021) and deactivation (Little et al., 2010; Marlowe & Berbesque, 2012), as well as the genetic and physiological substrates (Acevedo et al., 2020; Poeppl et al., 2016) of different components of mating psychology as expressed across sexes, personal circumstances, and socioecologies. Evolutionary behavioral scientists may also greatly benefit from widening their focus to include historical and newly emerging variations of gender/sex expression and identity (de Menezes Gomes et al., 2020; Pettersen et al., 2018; Schmitt, 2017), gender transition (Arístegui et al., 2018), sexual orientation (Bailey et al., 1994; Schmitt, 2007; Valentova et al., 2020), variations of sexual development (Berenbaum et al., 2018; Khorashad et al., 2018), and variations of personality functioning (Collazzoni et al., 2017) and explore how each of these intersect with culture and with each other to affect how mate preferences are expressed all around the world.

Conclusions

Evolved psychological sex differences have never been hypothesized to be "innate" in the sense that they are impervious to developmental, cultural, or socioecological influence (Buss, 1998). Indeed, almost all human psychological adaptations are designed to *expect* informative external inputs in order to function properly (Tooby & Cosmides, 1992). Evolved mate preferences are no different, and are not hypothesized to be expressed gender-essentially, gender-dichotomously, biologically deterministically, or culturally invariant around the world (Buss, 1989; Walter et al., 2020). As noted more than 30 years ago, "Evolutionary approaches to behavior, far from indicating that human behavioral patterns must be universal and 'wired,' actually provide us with good reasons for expecting cultural diversity and good tools for showing how it might develop. Even gender-role related behavior may be very variable. Highly 'macho' male behavior may be an adaptation to dangerous ecological and economic constraints" (Nisbett, 1990, p. 255). As Nettle (2009b) more recently concluded, "to endorse the central ideas of evolutionary psychology (and Darwinism more

generally) need in no way imply genetic determinism or de-emphasize the importance of culture … neo-Darwinism is not opposed to social and cultural determination of behaviour, but is a framework for understanding why such determination exists" (p. 224).

In this chapter, evidence was reviewed that confirms women are more likely than men to desire potential mates who possess cues to the *ability* and *willingness* to provide resources. Women tend to value cues such as status and prestige, ambition and work ethic, confidence and intelligence, honesty and reputation for generosity, slightly older age, and in some cultures, hunting ability, physical strength, body size, shoulder width, music ability, oratory skill, educational attainment, or other locally relevant armaments or adornments (Ellis, 1992; Stephen & Luoto, forthcoming). These preferences are not "essential" to being a woman, nor do they exist in all women from birth, but rather they emerge developmentally and are particularly heightened in certain types of women and in certain types of socioecologies. For instance, women who are especially feminine, who are physically attractive, and who possess resources themselves tend to value these cues more in potential long-term mates. Women tend to pay more attention to these cues when in harsher socioecologies and possibly when denied sociopolitical equality (cf. Walter et al., 2021; Zhang et al., 2019). Finally, individual and cultural circumstances appear to alter the relative importance of cues to men's *ability* to invest (i.e., masculinity) and cues to their *willingness* to invest (i.e., nurturance), leading women to engage in predictable trade-offs depending upon their personal circumstances and local socioecology.

In contrast, men more than women tend to value cues to youth and fecundity in potential long-term mates. Men tend to especially desire mates who possess cues such as facial neoteny and a low waist-to-hip ratio (Sugiyama, 2015). These preferences do not exist in all men from birth but rather emerge across development (e.g., via organizational or activational effects of hormones; Schmitt, 2017), and they are heightened in some types of men and in some types of cultures and socioecologies more than others. For instance, men who are particularly masculine, are wealthy, or possess higher testosterone express stronger preferences for youthful and highly fecund women. Findings across cultures are more mixed. Several studies have found men and women express stronger preferences for physical attractiveness within high pathogen environments (Gangestad et al., 2006), and some have found women's reactions to pathogens are stronger (Cantú, 2013; Luoto & Varella, 2021) leading to sex differences in physical attractiveness preferences being smaller in environments with high pathogen levels.

Future research will need to more clearly outline which specific cues of

women's physical attractiveness (e.g., full lips, wide eyes, relatively small jaw and chin, and 0.7 waist-to-hip ratio) men value more across differing conditions of environmental stress (e.g., high pathogen levels, high mortality, low safety, low general health, high population density, and skewed sex ratios). It is likely that different special design features underlie mate preference mechanisms (i.e., sensitivities to some inputs more than others) in both sexes and lead to their expression being heightened under differing socioecological conditions (Sng et al., 2018). Moreover, the full expression of mate preferences may emerge in dynamic interaction with other context-sensitive psychological adaptations, and there may be ontogenetic critical periods during which some mate preferences are more likely to be turned on or enhanced (e.g., by in utero or pubertal exposure to testosterone in men; Schmitt, 2017; or by women; Luoto et al., 2019). Both women and men are designed to be flexible and tactical mating strategists, and our felt sexual desires are likely going to be reactive as we confront different reproductive dilemmas (e.g., courtship vs. retention) and negotiate ever-shifting trade-offs linked to changes in our age, our mate value, and the qualities of our romantic partners (Arnocky et al., 2021).

Research on human mating around the world has revealed that several cultural contexts and socioecological conditions link systematically with features of human mating psychology. In environments with higher pathogen levels, for instance, humans are more likely to express stronger preferences for sex-typical traits (Little et al., 2007). Pathogens also appear linked to levels of polygynous mating, sociosexuality, fertility rates, and parental investment. Higher sex ratios (more men than women in a culture) are associated with more polyandrous mating, lower sociosexuality, lower divorce rates, higher levels of paternal investment in offspring, heightened male displays of masculinity, and heightened levels of risk-taking and intrasexual violence in men (Ackerman et al., 2016). Mate preferences, in some sense, are much like taste preferences and basic emotions of humanity, built upon a basic framework but experienced differently across cultures and socioecologies (Sorokowska et al., 2017). Human genes and the developmental processes that underlie mate preferences do not *determine* how people experience romantic desire, but they may *constrain* how women and men tend to do so. Importantly, these constraints happen in nonrandom ways that can be explained, in part, by the special design of human mate preference adaptations for receiving informative cultural and socioecological inputs.

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Notes

1. Humans do inhabit a special cognitive or sociocognitive niche among primate species (Pinker, 2010; Tooby & DeVore, 1987; Whiten & Erdal, 2012): we have likely undergone various degrees of self-domestication (Hare, 2017; Wrangham, 2019); we evolved a collective cultural brain, complex language, and an extended adolescence designed to amass and take advantage of cumulative cultural evolution (Henrich, 2016; Muthukrishna et al., 2018); and humanity's genetic and cultural variation has likely continued to coevolve throughout the Holocene to affect morality, social norms, and cultural institutions related to mating psychology (Laland, 1994; Richerson et al., 2021). However, these perspectives are not inconsistent with or opposed to the view that at least *some* sex differences exist in the special design of human mating psychology, and together these perspectives combined far outweigh the competing view of the standard social science model that men and women have evolved *absolutely identical* mating psychologies (Buss, 1995; Stewart-Williams & Thomas, 2013).
2. Related problems to "toxic tetrad" thinking include many scholars mistakenly assuming that evolved psychological adaptations must demonstrate extreme modularity across all explanatory levels (Barrett & Kurzban, 2006)—including conscious, functional, and physical levels of analysis (Brase, 2014; Pietraszewski & Wertz, 2021), that all human psychological adaptations evolved solely during the Pleistocene epoch (Hagen, 2015; Tooby & Cosmides, 1992), that all human psychological adaptations are generated solely from genes (Hagen, 2015; Tooby, 2020), that evolved adaptations justify problematic human behaviors (i.e., is-ought fallacy; Curry, 2006), the panglossian criticism that all human traits must be adaptations (Zagaria et al., 2020), among many others (for reviews, see Al-Shawaf et al., 2018; Jonason & Schmitt, 2016; Lewis et al., 2017; Winegard et al., 2014).
3. Mate preferences, if evolved, are not genetically deterministic (Zagaria & Zennaro, 2021). Mate preference mechanisms are designed to *expect* input from the environment (i.e., are designed to be thirsty for key actionable information from developmental, situational, dyadic, personal mate value, local socioecology, and other sources of information), are dependent on several forms of learning (e.g., content, target, and prestige learning biases), and are dynamically and disruptably influenced by other evolved psychological mechanisms (e.g., religious adaptations; Schmitt & Fuller, 2017). However, evolved mate preference mechanisms may result in predictable nonrandom constraints or modes of canalization on commonly observed variations of human mate preference expression (Barrett, 2001). The idea of any biological constraints or canalization on human mate preferences have led some to wrongly declare that evolutionary psychologists are genetic determinists and essentialists (Greene, 2020), one of many poisonous misrepresentations of evolutionary psychology (Al-Shawaf et al., 2018; Jonason & Schmitt, 2016; Stewart-Williams, 2018).
4. Psychologists often evaluate degree of sexual differentiation using the *d* statistic, with an observed *d* of ±.20 being considered a *small* sex difference, ±.50 is a *moderate* sex difference, and ±.80 is a *large* sex difference (Cohen, 1988). Negative *d* values typically indicate women score more highly on a particular preference, whereas positive values indicate men score more highly.

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PART II

Attraction and Mate Selection

CHAPTER
5

The Early Stages of Mate Selection

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Abstract

Given the centrality of mating and reproduction in the long course of human evolution, the selection of mates is a critical adaptive challenge that humans have needed to successfully confront throughout evolutionary history. This chapter provides an overview of major evolutionary theories of human mating, describes key hypotheses of mate preference psychology, and reviews relevant empirical research for the early stages of mate selection. We discuss mate preference adaptations for selecting both long-term and short-term mates, as well as methodological issues, controversies, and other developments that have, in recent years, surfaced in the mate-selection literature.

Key Words: evolutionary psychology, mate preferences, mate selection, long-term mating, short-term mating

Immensely accomplished business people seem to understand not only the ins and outs of the industries in which they have triumphed and prospered but also the importance of partner evaluation and selection. Berkshire Hathaway CEO Warren Buffet—one of the world's richest individuals over decades—pointed to meeting his late wife as key to his eventual success (Kunhardt, 2017), affirming a statement that he had made before: the most important choice in one's life is who one marries, and this point cannot be overemphasized (Gates, 2017). One of Silicon Valley's most powerful executives, Sheryl Sandberg, agreed, writing, "I truly believe that the single most important career decision that a woman makes is whether she will have a life partner and who that partner is" (Sandberg, 2013). On the opposite side of the relationship spectrum, former Cuban Prime Minister

Fidel Castro reportedly slept with 35,000 women—typically two a day, across four decades (GQ.com, 2016). Similarly, professional basketball player Wilt "The Stilt" Chamberlain told the world that he had enjoyed brief sexual relationships with 20,000 women: "I was just doing what was natural—chasing good-looking ladies, whoever they were and wherever they were" (Chamberlain, 1991). As the chapter describes, the selection of partners ranging from lifelong marriage partners at one extreme to anonymous one-night stands on the other extreme has important reproductive consequences and, as such, reflects the operation of adaptive mate preferences.

The early stages of mate selection have roots in people's evolved mate preferences and manifest in expressions of such preferences when people search for potential mates and when they meet and evaluate them for the first time. Accordingly, we review evolutionary psychological theory and findings on mate preferences for different types of relationships, covering how mate preferences —and mate preference priorities—are expressed in not only traditional surveys but also real-world contexts. We cover long-term and short-term relationships as well as provide an overview of some relationships that are neither entirely long term nor short term before discussing how people's mate preferences play out in modern-day venues such as speed-dating and the critiques that have been launched against the validity of mate preferences. Finally, we briefly look at how evolved mechanisms are now operating in evolutionarily novel environments, thereby leading to maladaptive mate selection.

The Evolution of Mate Choice and Preferences

Ninety-nine percent of the multicellular species in existence today reproduce sexually. Some such species are panmictic, like the global wanderer dragonfly (Troast et al., 2016) or the American eel (Wirth & Bernatchez, 2003), where individuals mate with random others in the population. However, many species have evolved to exhibit some sort of nonrandom mating or intersexual selection process (Andersson, 1994). Mate choice evolved in such species because certain traits are associated with greater reproductive outcomes for the individuals who choose their partners on the basis of those traits (Darwin, 1871).

Take giraffes, for instance. Male giraffes tend to prefer younger female giraffes who are closer to the age of sexual maturity (Pratt & Anderson, 1985). A male will rub against a suitable female's backside to induce urination. When the female urinates, the male will use his long tongue to taste it. The taste that the male evolved to prefer is precisely the one associated with estrus (Bercovitch & Deacon, 2015). If the in-heat taste is detected, the male then proceeds to follow

—stalk, as it would be considered in modern human society—the female, keeping other males at bay to the extent possible (Bercovitch et al., 2006). He establishes dominance over challengers by leaning his neck against theirs until one side gives up by pulling away first, with the neck fighting occasionally escalating to swinging their heads and necks to land blows on each other (Simmons & Altwegg, 2010; Simmons & Scheepers, 1996). Usually, one side concedes before anyone is significantly injured (Bercovitch & Deacon, 2015). Female giraffes tend to submit to male giraffes who prove themselves worthy through prolonged pursuit and dominance challenges, but they also seem to have preferences for males who are a few years older than the age when males can start reproducing (Pratt & Anderson, 1985). When a female identifies a preferred male, she may initiate relations by approaching him and rubbing his neck with hers (Leuthold, 1979). If he begins the Flehman sequence to induce her to urinate, she will usually forgo playing hard-to-get and, instead, get right down to sex.

Although humans do not usually follow the mate-selection rituals and customs of giraffes or other species, humans nevertheless differ widely within each sex in their reproductive value and thus, mating randomly would be far from optimal for reproductive fitness. Accordingly, to solve the adaptive problem of identifying partners who contribute positively to reproductive fitness, humans have evolved mate preferences on which to base their mate selection (Buss, 1989, 2016; Buss & Schmitt, 1993; Ellis, 1992; Symons, 1979, 1995).

In many species such as peacocks (Petrie et al., 1991) and mice (Roberts & Gosling, 2003), females exhibit mate choice but males do not (see Clutton-Brock & McAuliffe, 2009, for a review). This phenomenon has been largely attributed to the significantly larger minimum parental investment that females of most species are physiologically obligated to make than males (Trivers, 1972). Indeed, the sex difference in minimum obligatory parental investment exists in most if not all mammalian species, where females bear the costs associated with gestation and the nursing of offspring. Wherever females have a much larger minimum obligatory parental investment than males, females evolve to be more discriminating in their selection of mates to avoid incurring the costs of mating with (and being stuck rearing the offspring of) males who have low reproductive fitness (e.g., Haselton & Buss, 2000; Kenrick et al., 1990; Li & Kenrick, 2006). In turn, the less-investing sex—males in most but not all species—have evolved to compete among each other for access to the more reproductively valuable females (Trivers, 1972).

Long-Term and Short-Term Mating in Humans

For humans, whose relationships span the range from a brief sexual fling to lifelong marriage, the relative levels of minimally required investment from each sex and, hence, the degree of choice each sex has evolved to exhibit, depend on the intended mating duration (Kenrick et al., 1990). In this regard, much research has examined relationships at both ends of this spectrum, which include short-term sexual relationships and long-term, committed relationships (e.g., Buss & Schmitt, 1993; Gangestad & Simpson, 2000; Li & Kenrick, 2006; Thomas & Stewart-Williams, 2018).

Eagerness and Selectivity for Casual Sexual Relationships

Sex differences in minimum obligatory parental investment tend to be particularly pronounced in short-term relationships (Trivers, 1972). Throughout evolutionary history, if, say, a brief sexual encounter resulted in pregnancy, females would have needed to invest in nine months of gestation and, after childbirth, invest several more years to provide care and nourishment via lactation and breastfeeding to ensure offspring survival. In stark contrast, males are physiologically required to only contribute their sex cells, which can be replenished quite readily, and the brief time it takes to deposit the sex cells into the female during copulation. As such, if a poor mate choice is consummated, both the male and female gain similarly in terms of reproductive fitness, but males lose very little whereas females lose a lot and miss out on potentially more viable reproductive possibilities for up to several years (Daly & Wilson, 1983). Reflecting this cost-to-benefit discrepancy between the sexes, human females have evolved to be more hesitant and selective than human males when considering whether to enter sexual relationships and when evaluating the suitability of sexual partners (Buss, 1989; Geary, 2000; Kenrick et al., 1990; Li & Kenrick, 2006; Trivers, 1972).

Evidence from various sources supports this hypothesis (e.g., see table 1 in Buss & Schmitt, 2011; for a recent review, see Buss & Schmitt, 2019). For instance, numerous surveys have shown that men are more amenable to sexual relations than women (e.g., Ellis & Symons, 1990; Gray et al., 2019; Li & Kenrick, 2006; Lippa, 2009; Reiber & Garcia, 2010; Schmitt et al., 2001, 2003; Simpson & Gangestad, 1991) with meta-analytic studies also confirming this sex difference (Oliver & Hyde, 1993; Petersen & Hyde, 2010). Men's stronger orientation toward sexual intercourse also holds given any length of acquaintanceship from a few seconds (Clark & Hatfield, 1989) all the way up to

five years (Buss & Schmitt, 1993; Schmitt et al., 2001).

In a classic field study, physically attractive male and female confederates approached opposite-sex individuals and asked them to, that same evening, go out on a date, go back to their apartment, or go to bed with them (Clark & Hatfield, 1989). Roughly half the men and women who were propositioned agreed to a date, but the sexes significantly diverged as sex became more probable. For going back to a stranger's apartment, nearly two thirds of men agreed whereas only 5 percent of women agreed. When sex was directly requested, around three quarters of men agreed but zero women consented. Adding to this picture, the authors noted that men took the sexual requests in stride, asking if they could have sex earlier or reschedule for the next day. Men who declined also gave apologies or explanations (e.g., "I'm going with someone."). In contrast, women were more likely to be put off by the offers of intimacy (e.g., "What is wrong with you? Leave me alone."). Over two decades later, these findings were largely replicated in a sample of Danish college students (Hald & Høgh-Olesen, 2010) and, even more recently, a lab study using similar procedures (Tappé et al., 2013).

Relatedly, studies of sociosexuality, which refer to a person's behavioral tendencies and openness toward having casual sex, have indicated that, compared to men, women are significantly more sociosexually restricted, require more signs of love and commitment before having sex, and feel less positive toward sex without love (Oliver & Hyde, 1993; Petersen & Hyde, 2010; Simpson & Gangestad, 1991). This pattern has been demonstrated to be prevalent around the globe (Schmitt, 2005). The component of sociosexuality reflecting one's sexual desire (Penke & Asendorpf, 2008) is also closely associated to sex drive—one's desire or craving for sexual activity or pleasure (Baumeister et al., 2001), which is often estimated by the frequency of masturbation and orgasm—which, likewise, is higher in men than women (Ostovich & Sabini, 2004).

Indeed, these differences also show up in studies of fantasies of the mates who men and women select. Compared to women, men more frequently fantasize about sex on a daily basis (Ellis & Symons, 1990; Leitenberg & Henning, 1995). More than women, men fantasize about having sex with someone younger, strangers, people other than their spouse, and more than one person simultaneously (Joyal et al., 2015; Noorishad et al., 2019; Person et al., 1989; Wilson, 1997). In contrast, more often than not, women's fantasies involve notions of intense romance and idealize heroic and chivalrous men (Joyal et al., 2015; Rudman & Heppen, 2003) and involve one's current partner (Barclay, 1973). Thus, men's sexual fantasies are consistent with an evolved orientation

toward maximizing sexual access to fertile women while emotions and romance characterize women's fantasies and are consistent with their orientation toward longer-term relationships with highly investing partners (Buss, 2016).

Yet another line of evidence for the hypotheses above comes from studies of sexual intent perceptions, where men are thought to overperceive women's interest in a sexual relationship (i.e., sexual overperception bias; Haselton & Buss, 2000). In the original study by Abbey (1982), male–female pairs were assigned to observe an interaction between another male–female pair, before all four individuals rated the sexual intent of the female interactant. Men (both as observers and interactants) rated the female interactant's sexual intent as higher than her own rating. These findings have been replicated elsewhere (see Farris et al., 2008, for a review) and are consistent with the view that men have evolved an inferential bias to increase their motivation to pursue mating possibilities (e.g., Haselton & Buss, 2000). In contrast, given the reproductive benefits of being more discriminating in their mate choice, women have evolved to be (overly) skeptical of a man's commitment (Haselton & Buss, 2000; Henningsen & Henningsen, 2010), and underrepresent their sexual interest in a male partner (Perilloux & Kurzban, 2015; cf. Murray et al., 2017).

One study investigated people's minimum trait requirements (in terms of percentiles) for various types of relationships (Kenrick et al., 1990). One trait that was examined was intelligence. When considering dates, men and women both required someone with around average intelligence. As the level of involvement increased from date to one-night stand to casual sexual partner to steady partner to marriage partner, women increased their minimum requirements. Men exhibited the same pattern with an important exception: for purely sexual relationships, men's minimum requirements for intelligence did not increase but, rather, significantly dropped. For a one-night stand, required intelligence dropped close to the twentieth percentile level.

Thus, given the sexes' opposing strategies regarding casual sex and the benefits throughout evolutionary history of biparental investment in promoting offspring survival (Geary, 2000), men and women have evolved to enter long-term relationships with each other and to bond together in the care of offspring (Daly & Wilson, 1983). Given that both sexes potentially invest significantly in long-term relationships, both sexes have evolved to be equally choosy when selecting long-term partners. Despite the sex differences associated with short-term relationships, however, short-term relationships do occur, typically between women who are more sociosexually unrestricted and men who have the traits that women look for in short-term partners (Gangestad & Simpson, 2000).

Evolved Preferences for Long-Term Mates

There are substantial challenges to obtaining reproductive fitness that have likely shaped the evolution of mate preferences in long-term contexts. First, women are constrained by how their fertility varies with age. That is, women's fertility tends to peak by their mid-20s, decline after age 30, and drop to zero by age forty-five to fifty (e.g., Hawkes & Smith, 2010). Thus, a major adaptive challenge for men is to identify long-term partners who are of fertile age and have fertile years remaining (Buss, 1989; Buss & Barnes, 1986; Buss & Schmitt, 1993; Symons, 1979, 1995). In turn, it has been hypothesized that men evolved preferences for youthful partners (Buss, 1989; Conroy-Beam & Buss, 2019; Kenrick & Keefe, 1992), mainly by being attracted to various visual cues to youth and fertility (Manning et al., 1997; Singh, 1993; Sugiyama, 2015; Symons, 1979; Williams, 1975).

Men's fertility, in contrast, tends to decrease more slowly across the lifespan (e.g., Anderson, 1975; Nieschlag & Michel, 1986); thus, age does not constrain men's reproductive value as much as it does for women, although sperm counts and sperm quality do decline with age. As a corollary, women have not evolved as strong a preference for physical attractiveness as men have. However, a major adaptive challenge is that an offspring's ability to survive and thrive, especially in ancestral times, may be dependent on resources. Over evolutionary history, men have largely provided such resources. Indeed, paternal investment has been shown to make significant differences in children's survival and life outcomes in modern times (Geary, 2000, 2015). However, men's ability to access, accrue, and provide resources for offspring can vary quite widely (Buss, 2016; Conroy-Beam & Buss, 2019). Hence, women are theorized to place greater emphasis than men do on a potential long-term partner's social status, ambition, and industriousness —traits that broadly indicate long-term access to resources (Buss, 1989)—as well as traits such as hunting abilities that, at least in ancestral times, were important to offspring survival (Conroy-Beam & Buss, 2019; Buss et al., 2020).

In numerous surveys conducted over several decades, men, more than women, consistently consider physical attractiveness to be more important in a marriage partner, sexual partner, and romantic partners in general. Women, more than men, consistently consider resources and status-related characteristics to be more important in such relationships (e.g., Bech-Sørensen & Pollet, 2016; Buss, 1989; Buss & Barnes, 1986; Li et al., 2002; Sprecher et al., 1994; Walter et al., 2020; see Buss & Schmitt, 2019, for a review). Surveys have also confirmed that women generally prefer a slightly older mate, whereas men prefer a younger mate (Antfolk, 2017; Antfolk et al., 2015; Buss 1989; Conroy-Beam & Buss,

2019; Kenrick & Keefe, 1992). Similar sex differences in the relevant importance of physical attractiveness and social status on willingness to engage in different relationships have also been found in laboratory experiments using photographs, descriptions, and costumes to denote these traits (Townsend & Levy, 1990a, 1990b).

Although much research has focused on preferences for sex-differentiated characteristics, men and women have also evolved to equally value various other traits. Indeed, researchers have proposed and found that men and women similarly desire intelligence (e.g., Buss & Barnes, 1986; Buss et al., 1990; Kenrick et al., 1990; Li et al., 2002), creativity (e.g., Buss & Barnes, 1986; Li et al., 2002), warmth-trustworthiness (Buss et al., 2001; Fletcher et al., 1999; Valentine et al., 2020), good parenting (Lu et al., 2015), agreeableness (Botwin et al., 1997), and kindness and honesty (Barclay, 2010; Buss, 1989; Li et al., 2011). These traits may increase the likelihood that partners can successfully cooperate and solve problems that they encounter over the course of their lives (e.g., Barkow, 1989).

Another trait that has been shown to be equally desirable to both sexes is sense of humor (Feingold, 1992). This trait has been hypothesized as a sexually selected trait in which men evolved to display humor for women to evaluate (Miller, 2000). Indeed, whereas men tend to want a partner who is receptive to one's own humor, women are more likely to desire a partner who is able to produce humor (Bressler et al., 2006). Humor has also been hypothesized from an evolutionary perspective and shown to be used for indicating interest in potential partners during initial mate selection. That is, above and beyond the exchange of general conversation, people tend to initiate humor toward someone and respond positively to someone's humor when interested in that person for a potential relationship (Li et al., 2009).

Key Short-Term Mate Preferences

Although long-term relationships are ubiquitous, short-term relationships are also not uncommon. Large-scale surveys conducted by online dating site *Match.com* have consistently revealed that the majority of single Americans have had a one-night stand (e.g., Fisher, 2015; Jayson, 2012; Match.com, 2019) while, according to one review, between 60 percent and 80 percent of college students have had some sort of hook-up experience (Garcia et al., 2012).

For short-term relationships, obtaining a steady flow of resources from one's partner and cooperating over a long period of time to raise offspring are no longer relevant (Li & Kenrick, 2006). However, a man's genetic quality, which

may be indicated by his physical appearance, can still be passed on to offspring (Gangestad, 1993; Gangestad & Simpson, 2000). For men, even though overall standards go down for short-term relationships (Kenrick et al., 1990), the relative importance of obtaining a fertile partner goes up (Li & Kenrick, 2006). As such, both sexes have evolved to value physical attractiveness in a short-term partner more than in a long-term partner (Buss & Schmitt, 1993). Various mate preference surveys have shown findings that are consistent with these ideas, including those focusing not only on college students (e.g., Buss & Schmitt, 1993; Fletcher et al., 2004; Li & Kenrick, 2006; Regan & Berscheid, 1997) but also on adolescents (Regan & Joshi, 2003), adults (Buunk et al., 2002), non-Western samples (Li et al., 2011), and homosexual men and women (Regan et al., 2001).

The good genes argument stems from evolutionary biology, where various species have been found to choose mates on the basis of bilateral symmetry. Such species include zebra finches (Swaddle, 1996), bluethroats (Fiske & Amundsen, 1997), swordtail fish (Morris & Casey, 1998), Iberian rock lizards, (López et al., 2002), and rhesus macaques (Møller & Höglund, 1991). In humans, the simultaneous presence of symmetry and masculinity has been theorized to signal the presence of desirable genes. That is, because masculine features reflect high testosterone and testosterone tends to suppress the immune system, and because pathogens encountered during development can lead to bilateral asymmetry unless one has a strong immune system or genes that are resistant to pathogens, good genes may be at the root of someone who appears both masculine and symmetrical (Gangestad & Thornhill, 1997b; Møller & Thornhill, 1998). Indeed, symmetrical men tend to have more masculine faces (e.g., Johnston et al., 2001; Penton-Voak et al., 1999), are considered by women to be physically attractive (Scheib et al., 1999; Thornhill & Gangestad, 1994), and are more often selected as affair partners and sexual partners in general (Gangestad & Thornhill, 1997a; Thornhill & Gangestad, 1994).

Consistent with the good genes argument, it has also been proposed that women have evolved a preference for personality traits associated with underlying genetic quality in a short-term mate. Men with higher levels of testosterone display greater social dominance (Mazur & Booth, 1998), which is theorized to facilitate success in intrasexual competition (Ainsworth & Maner, 2012) and, hence, is preferred by women. Evidence supports such a hypothesis. Men with facial features associated with higher levels of testosterone (e.g., wider and shorter faces) are rated by women as more dominant and attractive for a short-term but not a long-term relationship (Valentine et al., 2014). Likewise, men who display socially dominant behaviors and personalities are rated as more

sexually attractive (Sadalla et al., 1987), especially as a short-term mate (Gangestad et al., 2004).

It should be noted, though, that access to genetically superior mates may not be the only reproductive benefit for women's short-term mating (e.g., Li & Kenrick, 2006, Study 5). One alternative theory is the mate-switching hypothesis, which proposes that women may have benefited from short-term affairs by cultivating backup mates, or to "trade up" for partners of higher mate value (Buss & Schmitt, 1993; Greiling & Buss, 2000; see Buss et al., 2017). Consistent with this view, independent lines of research show that women are more likely than men to fall in love with their affair partners (Glass & Wright, 1992), see being able to replace a partner as a benefit of affairs (Greiling & Buss, 2000), and are more interested in affairs when their primary partner is less successful (Gangestad et al., 2005). Although exploration of the mate-switching hypothesis has only recently gained traction (e.g., Buss et al., 2017), it nonetheless can shed further light on women's mate selection within the class of short-term relationships including infidelities.

Mate Preferences Have Priorities

By the end of the twentieth century, numerous studies had provided a clear picture of how preferences differ between the sexes. However, few studies examined how mate preferences differed *within* sex. Indeed, even though much empirical work had indicated that men value physical attractiveness more than women do and women value social status and resources more than men do, examinations of between-trait preferences within each sex across numerous decades showed that physical attractiveness was not all that highly valued over other traits by men and social status and resources were even less highly valued in comparison to other traits valued by women (Li et al., 2002; Powers, 1971). Yet, this pattern does not square well with the theorized adaptive significance of women's fertility or men's resources. After all, if a female partner is infertile or a male partner is destitute, mating, at least in ancestral times, would be a pointless endeavor.

To address this major disconnect between theory and empirical findings, Li and colleagues utilized a paradigm from consumer behavior/microeconomics (Li, 2007a; Li et al., 2002, 2011, 2013). Specifically, when people have very little disposable income, they tend to allocate their limited funds to goods and services that are most essential for basic living, such as cheap food; a small apartment; and access to water, electricity, and, in today's world, the internet. In economic terms, these *necessities* provide the most utility (usefulness to one's

life) when a person starts out with nothing. However, as more income becomes available, acquiring further amounts of necessities leads to increasingly less incremental benefits than would using the same money toward *luxuries*—things that are not essential for basic living but improve one's life once the basic things are in place. Classic luxuries include large-screen television sets, vacations, and private education.

The same prioritization process may apply to mate preferences in the mating market, where utility refers to reproductive fitness. That is, although many traits contribute to reproductive value, some will confer more reproductive value up front than others will, and, thus, people may have evolved to seek sufficiency on those traits first. That is, if women's physical attractiveness indicates fertility and men's social status indicates their ability to provide critically important resources in a long-term mating context, then men may have evolved to prioritize some physical attractiveness in a mate and women may have evolved to prioritize having some social status. However, as with economic necessities, once a moderate amount of physical attractiveness has been obtained and there is a reasonable level of assurance that a female partner is fertile, then diminishing incremental returns will set in and other traits will offer greater reproductive value. Similarly, once a moderate amount of social status has been obtained and there is a reasonable chance that resources will be available, further gains on social status will lead to increasingly smaller fitness gain than other traits will. For short-term mates, both sexes are hypothesized to prioritize physical attractiveness as a necessity, though, as described above, for different adaptive reasons (Li & Kenrick, 2006).

The mate preference priority model was tested using a budget allocation paradigm in which participants are given low, medium, and high budgets of "mate dollars" with which to design an ideal mate. Each mate dollar spent on a trait acquires a certain increase in percentile points on that trait. If a typical low budget were to be allocated equally across all traits, the resultant mate would have a very low level (e.g., twentieth percentile) of each trait. People, however, do not allocate their low budgets evenly. Consistent with the theory, for long-term mates, men tend to stack their low budgets in favor of physical attractiveness, while women tend to weight social status and resources (Li et al., 2002); for short-term mates, both sexes tend to prioritize physical attractiveness, though men do so more than women (Li & Kenrick, 2006). As budgets increase, however, less is spent on these traits in favor of acquiring other traits. As such, sex differences in preferences for these traits start out large at the low budget but diminish as budgets grow and choices are less constrained—a pattern that speaks to the often debated presence versus absence of sex differences in mate

preferences. This model has been replicated over the years (e.g., Choy et al., 2022; Jonason et al., 2012, 2017; Li, 2007b; Li et al., 2011; March et al., 2018; Thomas et al., 2020; Yong et al., 2019; Zhang et al., 2019; see Li et al., 2013, for a conceptual replication).

Social Confidence: An Underinvestigated Trait

Using a live-interactive paradigm, a recent study investigated the role of social confidence in initial attraction and mate selection (Li et al., 2020b). Male participants received training in person or via videos on how to handle speed-dating chats. Compared to those who received no training, men who received training felt more confident going into the chats, were perceived by their female partners to be more socially confident, more romantically desirable—especially for short-term relationships—and more worthy of future contact. Such men were also perceived to have greater social status and social dominance, though only social confidence itself was associated with greater romantic desirability.

The underlying idea is that displaying confidence in social situations may have evolved to be interpreted as an honest signal of a person's abilities in a host of contexts including mate selection. As such, the mechanism for trusting a display of confidence can be exploited in modern environments, where people deal with strangers whose qualifications cannot readily be verified—especially in one's initial interactions with a potential mate (Buss, 2016). Moreover, speed-dating is an evolutionarily novel activity about which people have relatively little intrinsic knowledge. Thus, people who receive pointers on how to handle speed-dating chats may be able to improve their confidence in such situations. This work, taken together with other surveys (Buunk et al., 2002) and experiments (Brand et al., 2012) and the vast number of books, seminars, and videos espousing the importance of confidence in attraction and other social situations, suggests that confidence is an important yet greatly understudied trait for mate selection and various other domains.

Attraction, Misrepresentation, and Deception

In the process of early mate selection, both sexes may engage in attraction tactics as well as deceptively misrepresenting themselves as more desirable than they really are. In this regard, the sexes tend to diverge in ways consistent with the theory outlined above. For instance, men tend to attract women by displaying and bragging about their resources and inflating reports of their own height to appear more masculine (Cheryan et al., 2015), whereas women tend to attract men by enhancing various aspects of their appearance (Buss, 1988).

Consistent with men's stronger inclination toward gaining sexual access, men more frequently lie about their commitment level with the intent of having sex (Fischer, 1996; Marelich et al., 2008). Indeed, contrary to popular conception but consistent with women's greater requirement for commitment before sex, men, not women, tend to confess love first in courtship, and men, rather than women, are happier to hear "I love you" before sex has occurred (Ackerman et al., 2011). Women, instead, misrepresent their physical attractiveness. The prevalence of the multibillion-dollar cosmetic and cosmetic surgery industries—mainly supported by women—attests to the effectiveness of these tactics (Buss, 1988; Li et al., 2012). Tooke and Camire (1991) found that whereas men tend to misrepresent their commitment, sincerity, and ability to acquire resources, women alter their looks to appear more physically attractive. Additionally, women more frequently attempt to deceive men about their physical attractiveness (Benz et al., 2005) and, among women between thirty-five and fifty (past peak fertility), tend to withhold from reporting their age in personal advertisements (Pawlowski & Dunbar, 1999).

Finally, both men and women may also enact the strategy of playing hard-to-get to artificially inflate their own perceived availability and mate value (Dai et al., 2013; Jonason & Li, 2013; Whitchurch et al., 2011). Particularly, women are more likely to employ such strategies (e.g., staying busy, not calling back, and not talking much) to induce further indications of commitment from a potential mate (Bowen & Gillath, 2020; Buss, 1988; Jonason & Li, 2013), which may be successful when used appropriately (Walster et al., 1973). Taken together, these findings indicate that what men and women misrepresent to each other, and why they misrepresent it in the initial mate-selection process, is largely consistent with evolutionary predictions about their mating psychologies.

Mate Choice in Relationships That Are neither Long-Term nor Short-Term

Although the long-term and short-term mating distinction or continuum has been instrumental in illuminating how mate preferences and mating strategies have evolved in response to different adaptive challenges associated with relationships that differ greatly in intended duration (Buss & Schmitt, 1993; Li & Kenrick, 2006), it does not, however, directly address the various relationship types that fall seemingly in between the two extremes (Jonason & Balzarini, 2016; Schmitt, 2015). For instance, a friends-with-benefits relationship (Bisson & Levine, 2009) involves casual sex between individuals who are friends and

may comprise as much as two thirds of the casual sex that college students are now having (Grello et al., 2006). Another prevalent type of relationship is the booty call, which involves casual sex among acquaintances that is often initiated through a text message (Jonason et al., 2009).

A few lines of evidence suggest that both these relationships may represent compromises between men's ideal desire for casual sex and women's ideal desire for committed, long-term relationships with partners who invest significantly (Choy et al., 2022; Jonason et al., 2009, 2010). For example, whereas men tend to be interested in friends-with-benefits relationships mostly for sex, women are more interested in the emotional connection that these relationships afford (Lehmiller et al., 2011). For booty calls, people value both physical attractiveness and kindness in partners (March et al., 2018). As with purely sexual relationships or one-night stands, booty call partners do not hold hands and they typically leave the scene after sex; yet, they frequently engage in romantic acts as long-term partners do, such as kissing (Jonason et al., 2010). Indeed, a key draw for women to take part in these hybrid relationships may be intimacy and the potential for a more long-term relationship (Jonason et al., 2009). These hopes may be somewhat misguided, though, as suggested by recent longitudinal evidence that most friends-with-benefits relationships do not actually transition into long-term relationships (Machia et al., 2020). More recently, some forms of infidelity have also been conceptualized as one form of such compromise relationships (Choy et al., 2022).

Another hybrid relationship is consensual nonmonogamy, which involves having multiple romantic relationships simultaneously (Jonason & Balzarini, 2016). Although these relationships are somewhat akin to a person having both a primary partner and one or more extra-pair affair partners, there is one key difference: in consensual nonmonogamy, all the involved partners know about and consent to the multiple-partner relationship. In these arrangements, primary relationships tend to resemble long-term relationships, whereas secondary relationships tend to resemble short-term relationships. For instance, primary partners in such relationships are rated as more desirable long-term mates (Mogilski et al., 2017) and are mate-guarded more than secondary partners (Mogilski et al., 2017, 2019). Indeed, people participating in consensual nonmonogamy tend to report greater investment in, satisfaction with, and commitment to their primary partner but more sex with their secondary partner(s) (Balzarini et al., 2017).

Real-Life Mate Selection

Whereas surveys and laboratory experiments mostly tap into ideal mate preferences and responses to hypothetical mate-selection scenarios, other methods have been utilized to study how people select mates in real life. Here, we review the various other methods that have been used to test evolutionary-based predictions of mate selection.

Personal Advertisements

Personal advertisements in newspapers and, more recently, online dating websites, are fruitful platforms in which to examine age and other traits being sought and offered in the initial stages of mate selection (e.g., Baize & Schroeder, 1995; Cameron et al., 1977; Grøntvedt & Kennair, 2013; Strassberg & English, 2015). In an early study, researchers analyzed 800 lonely hearts advertisements from a nationally circulated tabloid newspaper (Harrison & Saeed, 1977). Consistent with the findings of other such studies, women were more likely than men to offer attractiveness, seek financial security, and seek someone older. Men were more likely than women to seek attractiveness, offer financial security, and seek someone younger.

Analyzing both newspaper personal advertisements and marriage statistics, Kenrick and Keefe (1992) found that women in their twenties through sixties not only specified requirements for a mate around their own age up to ten years older, but they also married men in the middle of their specified age range. Men showed a different pattern. In their twenties, men preferred and married a mate around their own age, but as men got older, they preferred and married a mate who was increasingly younger relative to their own age. These findings have been largely replicated, with similar patterns found in online formats (Alterovitz & Mendelsohn, 2009; Dunn et al., 2010; Hitsch et al., 2010; Phua et al., 2018) and around the world (Dunn et al., 2010; Phua et al., 2018; de Sousa et al., 2002). A survey added a further nuance by finding that while teenage girls had similar age preferences for a dating partner as women, teenage boys, unlike men, were more willing to date older women and considered women who were several years older than themselves to be ideally attractive (Kenrick et al., 1996). Taken together, the overall pattern of findings on age preferences supports the view that whereas women have evolved preferences for a partner’s resources, which are more likely to be found in a somewhat older man, men have evolved to be attracted to partners who are reproductively viable. An in-depth review of this topic is provided in Conroy-Beam and Buss (2019).

Prostitution

In prostitution, the exchange of sexual access and resources is very direct. Consistent with men having evolved to be more eager for casual sex than women, men are much more likely to pay for sex than women are. Although some of the sex providers to men are other men, the vast majority are women (Brewer et al., 2000). Studies on prostitution in both Eastern and Western cultures show that prostitutes and escorts who are young, have a low body mass index, reasonably large breasts, and a waist-to-hip ratio near 0.7 tend to command higher fees for their sexual services than their older, larger, and less curvy counterparts (Dunn, 2018; Griffith et al., 2016; Prokop et al., 2020; Sohn, 2016). Likewise, mail-order brides, typically purchased from developing countries by men in more developed ones, tend to be significantly younger relative to their male counterparts than conventional brides are (Sohn, 2017). As such, when given significantly greater choice beyond what mate value affords in one's own mating market, men are seemingly guided toward the selection of younger, more fertile short-term and long-term mates.

Popular Media

The modern media that men and women regularly consume also reveals sex-differentiated preferences consistent with an evolutionary perspective (Barrett, 2010; Saad, 2012). For example, in American popular music, songs by male performers tend to advertise their wealth and status ("Billionaire" by Travie McCoy), focus on women's beauty (e.g., "You're beautiful" by James Blunt), or draw attention to women's desire for resources ("Golddigger" by Kanye West) while songs by female performers are more likely to focus on advertising their beauty ("All about that bass" by Meghan Trainor) and denigrating men who do not display commitment ("Bills, bills, bills" by Destiny's Child) (Saad, 2012). Far from being a modern phenomenon, similar patterns have been found in an examination of folktales from forty-eight cultures across the world, where male characters, more than female characters, were found to value a partner's physical attractiveness as the most important selection criteria. In contrast, female characters, more than male characters, were portrayed as emphasizing a partner's wealth and status as their main criteria (Gottschall et al., 2004).

Sex differences also emerge in people's consumption of erotic media (Hald, 2006; Salmon, 2012), the explicit visual contents of which are tailored to hijacking men's and women's mating psychology (Buss, 2016). Although both men and women view pornography, consumers of pornography are overwhelmingly represented by men. In 2019, more than two thirds of all visitors to Pornhub—the world's largest pornography website—were men.

Playboy, the men's lifestyle and entertainment magazine well known for its features of nude and seminude models, sold 5.6 million copies of its magazine in 1975 (Chemi, 2015); after going online, the brand has garnered over 15 million likes on its Facebook page. The women's equivalent, Playgirl, saw much less success; the magazine's popularity peaked in 1975 with more than 1.5 million copies sold (to a substantial proportion of gay men) and, today, is solely targeted toward gay men (Gellene, 1986; Rettenmund, 2017). Of the thirty most searched for porn stars in 2019, twenty-eight were women (Pornhub Insights, 2019). These lines of evidence are consistent with theorizing that men, more so than women, are drawn to pornography's visual focus on secondary sexual characteristics and visceral sex with strangers (Barrett, 2010; Ellis & Symons, 1990; Symons, 1979). Consistent with predictions of men valuing sex with large numbers of young and physically attractive women, men are also more likely than women to prefer pornography involving group sex (Salmon, 2012; Salmon & Fisher, 2018; see Hald et al., 2014).

In contrast, women, much more than men, consume romance novels and fall for its main characters, who have numerous strengths and qualities and engage in emotionally satisfying romantic love (Barrett, 2010; Cox & Fisher, 2009; Salmon, 2012). Just as pornography has been tailored to appeal to men's evolved preferences for physically attractive women and visceral sex, the contents of romance novels are tailored to appeal to women's mate preferences. Unlike the short-term and highly sexual nature of pornography, romance novels generally appeal to women's preferences for high quality, committed, long-term mates. Indeed, titles of romance novels typically include words relating to love and long-term commitment, while male characters and heroes typically have high social status (e.g., doctors and surgeons) and pronounced physical fitness (e.g., cowboys), and are on average seven years older than the heroine (Cox & Fisher, 2009; Salmon & Symons, 2003). Like most romance novels, the best-selling *Fifty Shades* book series appeals to women's evolved preferences: the protagonist Anastasia Steele, a young twenty-one-year-old fresh out of college, serendipitously encounters the mysterious, confident, and physically attractive Christian Grey, a billionaire entrepreneur six years older than herself. The two embark on a purely sexual, albeit sadomasochistic, relationship at first, which eventually blossoms into loving and committed marriage (at one point, Christian proclaims that Ana was the first woman who taught him how to love). In a befitting end, the series ends with the couple being happily married and preparing to celebrate the birthday of their young son. Not surprisingly, consumers of the trilogy of *Fifty Shades* films and books are mainly women (Illouz, 2014); on the opening weekend for the first *Fifty Shades* film, women

made up almost 70% of viewers and even outnumbered male viewers in some theaters by ten to one (Robbins, 2015).

Mismatched Mating and Nonmating

Underlying the phenomenon of pornography is the concept of evolutionary mismatch (e.g., Crawford & Anderson, 1989; Li et al., 2018; Tooby & Cosmides, 1990) whereby many psychological and physiological mechanisms are now operating in novel environments that differ from the ancestral environments in which they evolved. As a result, evolutionarily novel stimuli are now feeding into the mechanisms, inducing them to produce behavioral outputs that are no longer adaptive (Li et al., 2018).

In the nonhuman animal world, the Australian jewel beetle provides a good example (Gwynne & Rentz, 1983). Male jewel beetles have been found to be mating with beer bottles—stubbies—thrown out as litter in or around Durango on the western Australian coast. The bottles are brown and, to the male beetle, fairly big (larger female beetles carry more fertilizable eggs) and have small bumps near the bottom—supernormal versions of features that male beetles evolved to look for when flying over the arid ranges that constitute breeding grounds. So strong is the attraction toward the beer bottles that males attempting to mate with bottles will ignore actual females.

In the case of human mate selection, people are not only selecting video porn stars and those who are featured on websites as short-term sexual partners but are also getting married to sex dolls (e.g., P. Ellis, 2019), holograms (e.g., Miyazaki, 2020), and robots (e.g., Rawlins, 2017). Although these unconventional long-term mate choices will not lead to reproduction and, hence, are maladaptive, the mating choices reveal something about how evolved mate preferences are now functioning. High-end sex dolls, which are typically consumed by men, offer customized—and often supernormal—versions of secondary sexual characteristics and provide unlimited sexual access—key features to which men's mate-selection mechanisms have evolved to respond positively. Holograms are not tangible but can offer other desirable traits, as shown by Hatsune Miku, a "moe anthropomorph" designed to resemble a miniature teenage girl with attractive, youthful features, a sweet voice, and a caring personality. This particular hologram made the news when Tokyo resident Akihiko Kondo held a formal ceremony that cost two million yen for his marriage to Hatsune.

More generally, Japan presents another interesting mating-related phenomenon: more and more men are not participating in the mating market.

According to one survey, approximately 70 percent of young Japanese men claim a disinterest in both sex and romantic relationships (Meiji Yasuda Institute of Life and Wellness, 2017). Japan's declining fertility rate, one of the very lowest in the world and well below replacement level, is thought to be related to these so-called *herbivore men* (Deacon, 2013). Analyses from sociologists regarding this phenomenon are consistent with an evolutionary mismatch perspective on mating: women have a tendency toward hypergamy—desiring partners at least as educated and with more financial resources than themselves (Yu & Hertog, 2018). Given the increasing economic independence of women, the education and income expected of men is now too high for mates to be selected, thereby leading to a "marriage squeeze" (Qian & Qian, 2014). This dynamic is compounded in Japan, where the economy, including the large firms that provide men with substantial income, has been in a downturn for several decades.

Beyond Japan, low fertility is a phenomenon that all East Asian countries, many European countries, and several other countries around the world are facing and may have its roots in mismatched mating and mate selection (Li et al., 2018; Li et al., 2020b). More broadly, as technology progresses, it is likely that mismatch will become increasingly prevalent in mate choice—for humans and nonhuman animals alike, and will thus offer an increasingly fruitful area for understanding how mate evolved mate-selection mechanisms interact with environmental inputs to yield mate-selection behaviors.

Online Platforms for Early-Stage Mate Selection

Since around the onset of the twenty-first century, rapid technological advancements have provided new platforms for mate selection. People can post profiles of themselves and search through databases of hundreds if not thousands of potential mates. They can also establish communication and become acquainted with new individuals in no time. Although new methods were initially attached to negative stigma (Comunello & Parisi, 2020), electronic platforms (e.g., dating websites and social media websites) have become increasingly commonplace. In a recent survey, roughly half of young American adults indicated that they have used a dating site or application. Approximately 12 percent have married or been in a committed relationship with someone they met through a dating site or app (Pew Research Center, 2020).

Online dating behaviors generally reflect the expression of the same preferences that were present before the digital age. For instance, men seek younger partners online, whereas women seek older partners (Alterovitz &

Mendelsohn, 2009; Burrows, 2013; Conway et al., 2015; Kreager et al., 2014; Phua et al., 2018). Women indicate being more likely than men to make an effort to create a more physically attractive profile (McWilliams & Barrett, 2014), and, more than men, women overrepresent their physical attractiveness (Lo et al., 2013) and underreport their weight (Hall et al., 2010).

Men offer more social status-related information in their self-descriptions than women (Lee et al., 2019), whereas women are more likely to seek status-related information in profiles than men (Alterovitz & Mendelsohn, 2009). Women, but not men, indicate preferences for partners who are highly educated (Neyt et al., 2019; Ong, 2016). In a study conducted in China, numerous fake male and female profiles varying in reported income levels were posted on a dating website. Male profiles with higher income received more visits from women, but visits to female profiles were unrelated to income (Ong & Wang, 2015). Likewise, a large study of more than forty thousand actual dating profiles found that women were more explicit in specifying the exact level of educational attainment required of a potential mate than men were, and the minimum levels stated by women were higher than those stated by men (Whyte et al., 2018). Not surprisingly, men, more than women, overstate their income and education in their online profiles (Hall et al., 2010).

Speed-Dating

As described in the preceding section, there are various evolutionarily novel contexts in which mate preferences are being expressed in ways consistent with evolutionary predictions. However, some ostensibly conflicting findings from research on one modern mating practice—speed-dating—has led to a vigorous debate in the last decade or so about the validity of mate preferences.

Speed-dating is a mating practice that gained significant popularity in the 2000s. At the typical speed-dating event, previously unacquainted men and women chat with each other in a series of short “dates,” usually up to five minutes each. After each chat, individuals indicate their interest in pursuing further contact with the other person. For mate-selection researchers, speed-dating offers a live, interactive field-study venue where both members of each dyad simultaneously display their own romantic potential while assessing the suitability of a potential date (Finkel et al., 2007). By comparing pre-event survey methods and behavioral outcomes of numerous interactions, the speed-dating paradigm also allows researchers to examine the extent to which reported mate preferences map onto actual mate-selection criteria. However, as described below, various studies conducted on speed-dating in recent years have produced

varying findings.

CHALLENGING THE VALIDITY OF MATE PREFERENCES: MIXED FINDINGS IN SPEED-DATING STUDIES

An early study on speed-dating examined the preferences of more than ten thousand men and women who participated at speed-dating events organized by the now-defunct HurryDate (Kurzban & Weeden, 2005). In contrast to predictions made from an evolutionary perspective, men and women did not differ in their preference for physically attractive or high social status speed-dates. Instead, for both sexes, physical attributes—such as height, age, an attractive face or body—predicted whether speed-dates were chosen, while a potential date's education and income were unrelated to men's and women's choices.

Subsequent studies provided equivocal support for evolutionary predictions. One study of speed-dating events attended by graduate and professional-school students at Columbia University showed that men's decisions to "yes" speed-dates were predicted by a speed-date's physical attractiveness; for women, their decisions were better predicted by a speed-date's intelligence (Fisman et al., 2006). Similarly, one speed-dating study conducted in the United Kingdom revealed that women were more likely to select partners with professional or managerial jobs than men were (Lenton & Francesconi, 2010). On the other hand, other studies reported evidence to the contrary. Although one study found that women (but not men) based their yes decisions on a partner's income, the researchers failed to find a difference in the extent to which men and women based their yes decisions on a speed-date's physical attractiveness (Asendorpf et al., 2011). Similarly, an American study found that both men and women equally based their yes decisions on a speed-date's physical attractiveness (Luo & Zhang, 2009), and a German study found that people's reported preferences for traits such as physical attractiveness, status, and others poorly predicted their actual choices (Todd et al., 2007).

In a speed-dating study conducted at Northwestern University, Eastwick and Finkel (2008) found little evidence that people's stated mate preferences aligned with their evaluation of speed-dates during and after the event. Although men based their yes decisions more on a speed-date's physical attractiveness than women did, men and women did not differ in the extent to which a speed-date's physical attractiveness or earning prospects influenced their romantic desire for or chemistry with a speed-date. On the basis of these findings, the researchers challenged the validity of mate preferences and thus, the evolutionary perspective, and subsequently produced a meta-analysis showing little evidence

for preferences predicting actual mate choice where people meet in person (Eastwick, Luchies, et al., 2014b).

MEETING THE CHALLENGE: IMPORTANT CONSIDERATIONS FOR EVOLUTIONARY MATE PREFERENCES RESEARCH

The explanation provided in the challenges—that mate preferences can work for hypothetical situations but do not apply when potential mates actually meet—runs counter to decades of evidence derived from multiple cultures and time points and using various sources and methods. Indeed, various mate preference scholars have pointed out problematic methodological decisions and theoretical interpretations in these seemingly disconfirming studies (e.g., Campbell & Stanton, 2014; Fletcher et al., 2014; 2020; Li et al., 2013; Li & Meltzer, 2015; Meltzer et al., 2014a, 2014b; Schmitt, 2014).

ISSUES WITH SPEED-DATING STUDIES

Li et al. (2013) argued that the apparent lack of sex differentiation in mate choices reflects an artifact of speed-dating events, which typically fail to include representation from potential mates at the low end of desirable traits such as physical attractiveness and earning potential. That is, people who sign up for speed-dating events—typically those who can afford private education and professionals to whom speed-dating events are marketed to—have a reasonable level of social status. In contrast, people who have a low earning potential may stay clear of such events. Without fully representing the variation—particularly, the low end—of these key traits, the influence of these traits may be less pronounced. Such an argument is consistent with the mate preference priority model, which indicates that men and women evolved to prioritize avoiding people who are too low on physical attractiveness and social status, respectively, and, hence, the critical sex differences are most likely to emerge at the low- to mid-range of these traits (e.g., Li & Meltzer, 2015).

Li et al. (2013) presented a series of studies supporting these conjectures. Participants were assigned to speed-date individuals prerated as low or moderate on physical attractiveness or social status. Consistent with the mate preferences priority model and, more broadly, evolutionary predictions, experimentally manipulating these key traits revealed significant sex differences in mate choice: men's evaluations and decisions depended more on a speed-date's physical attractiveness than women's were, and women's evaluations and decisions depended more on a speed-date's social status than men's were.

Furthermore, and in contrast to Eastwick and Finkel (2008), mate preferences also predicted how men and women evaluated and chose their partners. For

participants who rated physical attractiveness as more important (compared to less important), their evaluations of a partner's desirability and acceptability depended more on the chat partner's physical attractiveness. The same held true for social status. Men's and women's mate choices further depended on the mating context. Whereas a sex difference emerged in men's and women's considerations of a partner's suitability for a long-term relationship, such that men's (women's) considerations depended more on a partner's physical attractiveness (social status), both sexes rejected partners with low physical attractiveness when considering a short-term relationship. Moreover, these results were consistently significant in the predicted directions when analyses were based on manipulated trait levels, less consistently significant when analyses were based on participant-perceived levels of a manipulated trait, and even less so when analyses used participant-perceived levels of a trait that was not manipulated. This indicated that null findings in previous speed-dating studies—where the trait levels of speed dates were not manipulated and were based on participant-perceived trait levels—likely reflected a lack of variability in the pivotal traits being tested (Li et al., 2013).

Meltzer et al. (2014a, 2014b) outlined three criteria (and consequently, seven methodological standards) for designing valid tests of sex differences in mate choice. Of the 97 studies included in the meta-analysis by Eastwick et al. (2014b), Meltzer et al. (2014b) noted that only one had sufficiently met these criteria. They then presented four longitudinal studies of married couples addressing these limitations and obtained results consistent with evolutionary predictions. Subsequently, Eastwick et al. (2014c) argued that the criteria and standards proposed by Meltzer et al. (2014b) were conceptually weak and offered new analyses (that purportedly met all these criteria) and documented found little evidence supporting sex-differentiated mate choice. In a rejoinder, Meltzer et al. (2014a) argued that, despite claims by Eastwick et al. (2014a), their reanalysis and critique remained improperly calibrated to detect sex differences in mate choice. Similarly, Schmitt (2014) raised several conceptual and methodological issues with Eastwick et al.'s meta-analysis, to which Eastwick et al. (2014a) countered with their own claims.

On the Predictive Validity of Ideal Preferences

Fletcher et al. (2014) investigated the conclusion by Eastwick et al. (2008, 2011) that people's explicitly reported ideal mate preferences poorly predict actual mate choice. Using a live interaction paradigm, male–female student pairs were assigned to 10-minute conversations. Consistent with an evolutionary

perspective, women were more selective (i.e., less likely to yes interaction partners). Furthermore, this sex difference was mediated by women's perceptions of their interaction partners as failing to match or exceed their own ideals. Likewise, both Campbell et al. (2016) and Gerlach et al. (2019) examined the predictive validity of people's ideal preferences (before entering a relationship) on their actual partner's characteristics five months later; both studies found that people's ideal preferences predicted the characteristics of later partners.

Li and Meltzer (2015) reviewed the debate and described various reasons why mate preferences might be disconnected from actual mate choice (e.g., trait information asymmetry, mating context ambiguity, and trait measurement). Similarly, Conroy-Beam and Buss (2016a; 2016b) argued that the low correlations between people's stated preferences and actual mate choice reflected the inherent complexity and constraints of mating markets. For instance, mate choice is not only dependent on one's preferences but also one's own mate value. Using an agent-based model, they documented a link between mate preferences and mate choices in newlywed couples (Conroy-Beam & Buss, 2016a), and that more desirable individuals (i.e., of higher mate value) were more likely to successfully exercise their mate preferences (Conroy-Beam & Buss, 2016b).

The debate regarding the validity of (evolved) mate preferences remains a spirited one, with recent research furthering arguments on both sides (e.g., Eastwick & Smith, 2018; Valentine et al., 2020). Eastwick et al. (2019) recently attacked common approaches for testing the predictive validity of ideal preferences and proposed a set of "best practices" for doing so. In reply, Fletcher et al. (2020) critiqued Eastwick et al.'s analysis and recommendations and provided evidence attesting to the predictive validity of people's ideal mate preferences. Valentine et al. (2020) confirmed the utility of predicting mating outcomes (e.g., partner selection and marital satisfaction) using individuals' ideal preferences for the trait of warmth-trustworthiness. Going forward, further research is needed that does not ignore the wealth of theory and empirical findings on mate preferences and mate selection from an evolutionary perspective. The perspective that human mate preferences must always translate into actual mate choice is naïve, given that who one chooses as a mate is a complex affair that depends on a multitude of variables such as one's priorities, mate value, competition, and the information available about potential mates. Future scholarship that carefully considers the interplay between these variables will further enlighten how various behaviors can be produced by the (mismatched) interaction between psychological mechanisms and novel environments.

Conclusion

Mate selection occupies a critical position in mating and comprises both the mate preferences that evolved to guide the selection process and the intersexual selection process itself. As reviewed in this chapter, humans have evolved mate preferences that allow them to initially select mates who are likely to contribute to reproductive fitness through the provisioning of fertility, good genes, resources, or other qualities. While human mating has been fruitfully organized along the lines of long-term and short-term mating, there are relationships that seem to increasingly occupy spots on the duration continuum in between these two extremes. Moreover, a particularly important source of influence on mate selection involves the significant changes in mating environments that are being induced by rapid technological progress. Such change induces a mismatch between the inputs that are now being processed and those that the mechanisms evolved to process and may lead to radically different or maladaptive mate-selection outcomes. While mate-selection patterns may be increasingly complex, researchers will also have more opportunity to understand how evolved psychological mechanisms process environmental factors.

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CHAPTER
6

Computational Models of Mate Choice

Daniel Conroy-Beam

Abstract

Given mating's close proximity to reproduction, human mate choice psychology would have recurrently both posed and solved critical adaptive problems. These same problems pose myriad computational challenges. Selecting a mate requires evaluating potential partners across multiple dimensions, summarizing these evaluations, and using finite resources to navigate mating markets occupied by mating rivals and potential mates with unknown interests. To make things harder, predicting mate choice behavior requires predicting through the interaction of these many processes, scaled up to the market level. Computational models provide researchers ideal tools for studying these otherwise intractable systems. With computational modeling tools, mating researchers can simulate the dynamics of complex mating markets and compare predictions of alternative models to real behavior. This chapter reviews the literature on computational models of human mating, with special emphasis on models of mate preferences, mate evaluation, and mate selection. It focuses on the computational problems inherent to human mate choice, models of how mating psychology solves these problems, and empirical data that speak to the plausibility of these models.

Key Words: computational modeling, mate preferences, mate value, mate selection, agent-based modeling

Human mate choice poses a complex decision problem. Selecting a mate requires evaluating potential partners who vary across multiple dimensions, distilling these multiple evaluations into summaries useful for decision-making,

and using finite resources to navigate mating markets occupied by both mating rivals and potential mates whose interests, desires, and commitments are at least partially unknown. These processes play out across multiple decision makers embedded within dynamic mating markets, where one person's decisions can affect the decisions available to everyone else. These processes are of great importance for human life and human evolution and so have attracted intense research interest for decades. And yet, precise descriptions of the nature of human mate choice remain elusive.

In this chapter, I argue that computational models provide researchers ideal tools for studying human mate choice. This chapter identifies the limitations of traditional verbal theorizing approaches with respect to understanding human mate choice and the advantages provided by computational models. Furthermore, the chapter reviews the literature on computational models of human mating, with special emphasis on models of the mate preferences, evaluation, and selection. In doing so, this chapter provides a rationale for the application of computational models and an overview of the state of computational models of human mate choice, as well as a roadmap to those areas of research in need of more and more sophisticated computational models of human mating.

What Are Computational Models and What Are They Good For?

Appreciating the need for computational models in the study of human mate choice requires understanding both how they differ from other modeling approaches and the strengths and weaknesses afforded by those differences. In this chapter, "computational model" refers to any model that attempts to describe the nature of human mating psychology by emulating the computations it performs. Computational models can take a variety of forms. One particularly relevant form is "agent-based modeling." Agent-based models are computer simulations of social systems. They simulate populations of autonomous individuals who interact with one another and their environments on the basis of preprogrammed decision rules (Wilensky & Rand, 2015). For computational models of human mating, agent-based models are most often used to construct simulations of mating markets, where agents representing individual people pursue one another as mates according to decision rules specified by alternative mate choice theories.

How can these models be useful to mating researchers? To see why, it can be helpful to think about the nature of theorizing within most mating research. Most theorizing in human mating research is verbal: roughly, upon identifying a

phenomenon in need of explanation, the researcher articulates in words a hypothesis that they think could account for the known facts. Then, through counterfactual thinking, causal reasoning, and informal logic, the researcher imagines possible worlds in which their hypothesis is true or false and postulates what those worlds would be like. Finally, the researcher compares the real world to these imagined possible worlds. To the degree that the real and possible worlds correspond, and especially to the degree that the imagined worlds point to previously unknown facts about the real world, the researcher's hypothesis gains support.

Verbal theorizing is a powerful method of scientific theory building and as such has been the dominant method of theorizing throughout most of psychology. Nonetheless, verbal theorizing also does have some important limitations, some of which are acutely relevant to studying human mate choice. The first is that verbal theorizing is particularly challenging for building theories about complex systems. Consider a simple example: men around the world have been routinely observed to prefer physical attractiveness in potential partners more than do women (Buss, 1989; Walter et al., 2020). What should this fact predict about men's mate choice behavior? One intuitive possible prediction is that men should more often choose physically attractive mates. However, consider also that men have other mate preferences—for kindness, intelligence, good health, and so on—that may sometimes countervail their physical attractiveness preferences. After all, there is no guarantee that the most physically attractive mate in one's local environment is also the kindest. One might think that, on average, in the long run, men overall would tend to select more physically attractive partners, but among any small set of potential mates, trade-offs among preferences may lead men to forgo more attractive mates in favor of partners who offer a better overall balance of endowments. Furthermore, human mate choice is mutual, and physically attractive women, presumably knowing that they are in higher demand, tend to set higher standards (Buss & Shackelford, 2008). Knowing this, men who are not up to those standards may choose to not waste their time pursuing highly attractive mates who will ultimately reject them, meaning preferences and behavior may line up only for the most desirable men.

Men's real choice behavior will result from the balance of these and other competing forces. But how, from the armchair, can we determine where that balance point will be? It is difficult, relying just on intuition, to account for all of the relevant interacting processes and constraints and to derive precise predictions. Evidence of this difficulty comes from disagreements within the human mating literature itself. Most recent debates around human mating have

centered on disagreements over what predictions actually follow from mate choice theory: for instance, whether mate preferences should be associated with relationship quality (Eastwick et al., 2014; Schmitt, 2014), whether choices in traditional speed-dating paradigms provide adequate reflections of real-world mate choice (Li & Meltzer, 2015), and whether the effects of mate preferences manifest exclusively in interactions between mate preferences and partner qualities (Eastwick et al., 2019; Fletcher et al., 2020). The prominence and persistence of such theoretical debates over the most basic predictions of mate choice theory betrays the difficulty of verbal theorizing about human mate choice.

A second important limitation of verbal theorizing is that it can inhibit effective scientific communication because verbal theorizing is inherently private, opaque, and ambiguous. Predictions from verbal theories derive from reasoning processes that occur inside researchers' heads. Other researchers are not directly privy to the details of those processes. This is problematic because researchers are not necessarily consciously aware of all the assumptions that they are making in order to derive their predictions, nor do they necessarily articulate all of the assumptions that they are aware of. And even among those articulated assumptions, confusion can still arise because language is inherently ambiguous. Above I articulated a prediction derived from a verbal mate preference hypothesis: "that men should more often choose physically attractive mates." But what does this mean? Does this mean that men should more often choose physically attractive mates compared to physically unattractive mates? Or that men should be more likely to choose physically attractive mates than are women? And what will the magnitude of this difference be? Will there be a linear relationship? Or an exponential relationship? Or a stepwise function? Any of these interpretations could be consistent with that single utterance—and different researchers can and will interpret that same phrase differently.

Of course, not all verbal models are as ambiguous as this intentionally exaggerated example—many verbal models can be quite precise and quite useful across domains of scientific study. But all verbal models contain some degree of ambiguity. And especially with a topic of study as multidimensional as human mate choice, any interpretive wiggle room granted on the individual dimensions of theorizing translates into exponentially larger spaces of confusion in the realm of predictions. This inherent ambiguity of verbal models, compounded by the private nature of researchers' true reasoning processes, can make it challenging to communicate theory in a transparent and unambiguous manner.

Computational Models Help Solve the Limitations of Verbal Theorizing

Computational models can help address some of the limitations posed by verbal theorizing. A common mistake is to think of computational models as a source of data—as a means of *testing* hypotheses. This, generally speaking, is incorrect. Rather, computational models are an alternative method for *expressing* hypotheses. In a computational modeling framework, in contrast to a verbal theorizing framework, rather than merely imagining worlds in which a hypothesis is true, a researcher uses computer code to literally create simulated worlds in which a hypothesis is true. The researcher can derive predictions from a hypothesis by directly observing the features of its simulated worlds. What are the advantages of this computational modeling approach? There are many; chief among them: computational models are less ambiguous and more transparent than verbal models.

Unlike verbal theorizing, computational modeling renders prediction generation unambiguous. Whereas humans can struggle to keep track of the many processes that are implied by a given hypothesis, computers have no such limitations. Computer code executes literally and logically, with no forgetting, confusion, overlooking, bias, arithmetic errors, or other potential human missteps in theorizing. As such, computational models act as "logical machines" designed to automatically convert theoretical assumptions into predictions (Gunawardena, 2014), cutting out the human middle man and therefore the possibility for human error.

This cold, logical nature of computational models makes it unambiguous what predictions do and do not follow from a given hypothesis. Any features of a model's simulated worlds constitute predictions that follow from that model. To the extent that these features comport with features of the real world—and to the extent that this is truer of a given model more than it is of alternative models—the hypothesis embedded within that model is supported. Any features that are not present in a model's simulated worlds are predictions that do not follow from that model's hypothesis. If a model's simulated worlds fail to reproduce some important feature of the real world, this indicates that the model is somehow inadequate: either its programming or its assumptions need to be adjusted so that it makes the correct prediction. Fine-tuning computational models to make more accurate predictions thus provides an opportunity for objective and systematic theory development.

Computational models additionally facilitate communication in ways that verbal theories do not. In contrast to the private reasoning inherent to verbal theorizing, the logic of computational models is public and transparent because all "reasoning" in computational models occurs by execution of computer code. The outcome of a computational model depends only upon the computer code

used to generate it. Any implicit assumptions omitted from this code will fail to contribute to its predictions until they are made explicit and incorporated within its code. Any mistaken assumptions or programming errors will execute and cause undesirable behavior until they are identified and corrected.

Furthermore, such technical or theoretical errors are more likely to be identified in a computational modeling framework because computer code, unlike private reasoning processes, can and should be made publicly available to others. Other researchers can therefore scrutinize and modify computer code to improve its assumptions. By editing model code and observing the changes in a model's behavior, other researchers can see for themselves whether a model actually produces the predictions its creator claims that it does; they can assess whether crucial assumptions have been omitted and can insert those assumptions into the model's code; they can determine whether some assumptions are superfluous and can remove them from the model; and they can identify assumptions that are incorrect or misleading and replace them with better assumptions. These modifications will result in new hypotheses that make new predictions which can be compared against real-world data to determine the empirical standing of the revised ideas. As such, computational modeling makes possible transparent, reproducible, collaborative, and open theorizing in a way not possible with verbal theorizing alone.

Applying Computational Models to Human Mating

How specifically can we harness the many potential benefits of computational modeling to better understand human mate choice? In attempting to model any psychological phenomenon X, an often-useful framing question is "How could I build a robot that does X?" Many complex systems can appear simple to understand from the outside because we do not know what we do not know about a system's inner workings. However, the limits of our knowledge are harder to miss once we sit at the workbench and attempt to build a new system that emulates our system of interest. In doing so, we encounter all the problems our real-world system encounters and must articulate specific, functioning subsystems for solving those problems. To the extent that we cannot solve these problems and reproduce our real-world system of interest, we know that we are missing something important about the real world. Attempting to reproduce real-world systems rather than merely describing them from the armchair is therefore a stricter test of our knowledge because it holds our theories accountable to real-world consequences. Or, as Richard Feynman put it, "What I cannot create, I do not understand."

The value of attempting to re-create rather than merely describe systems of interest was best exemplified by the "summer vision project": an attempt, in the 1960s, to create a computer vision system as a summer research project. The researchers behind this project hoped to have, within two summer months, a computer system that could, when given visual information, distinguish foreground and background and recognize diverse objects including cigarette packs, cups, balls, and tools (Papert, 1966). In retrospect, this was an outrageously ambitious project as computer vision is still an unresolved problem sixty years later. In terms of producing computer vision, the project was a complete failure. However, the project was a major success in that it revealed challenges inherent to human vision that were previously unknown and charted a course for future vision research.

So, to follow in this spirit in the context of human mate choice, the question becomes: "How can we build a robot that selects mates in the way that humans do?" This question helps to highlight the challenges this mate choice robot will encounter on its path to mating success as well as the information-processing systems the robot will need to surmount these challenges. For the remainder of this chapter, I focus on three important such challenges, models of systems that have been proposed to solve these challenges, and relevant empirical evidence for the existence of these systems in the human mind. This review is by no means exhaustive—of either the challenges the robot would face or the potential solutions. Ideally, it is nonetheless illustrative.

Human Mate Preferences: Distinguishing Potential Mates

One of the very first challenges the mate choice robot will encounter is effectively discriminating between potential mates. Mating effort is finite: the robot will have only so much time and so much energy that it can dedicate to mating as opposed to other important processes such as growth, body maintenance, immune functioning, parenting, and so on. The finite nature of mating resources is what necessitates mate *choice*: pursuing one mate expends resources that could have been spent pursuing another, and so the robot most prioritize some potential mating opportunities over others. How can the robot accomplish this prioritization effectively?

This is no trivial task. In stepping into the mating market, the robot will encounter an array of potential mates who vary along an infinite number of dimensions. Potential mates will vary in their height, their weight, their odor, and the number of moles on their left legs; they will vary in their kindness, intelligence, conscientiousness, and horoscope; and they will vary in their

endowment of financial resources, social connections, accumulated cultural knowledge, and the sizes of their seashell collections. Worse, for any given dimension, there are infinite transformations that the robot could consider: why attend to a potential mate's height as opposed to their height squared? Or cubed? Or height to the 2.5th power, or 2.25th power, or 2.125th power, and so on. Even if we can take for granted that the robot is able to distinguish viable potential mates from nonviable mates (e.g., a young, heterosexual female robot should likely exclude postmenopausal females from consideration), there is still literally no end to the number of ways the robot could, in principle, rank order their potential mating options.

For at least two reasons, the robot cannot consider all the ways in which their potential mates differ. First, the space of possible considerations is infinite, but the robot must make a choice in finite time and with finite computational resources. So, just as the robot must prioritize some potential mates over others, it also must prioritize some dimensions of variation over others in evaluating potential mates. Second, the consequences of each consideration are not the same on the most relevant metric: the relationship between variation along a dimension and reproductive success. As with any dimension of biological variation, the overwhelming majority of variations among potential mates are likely to be neutral with respect to the robot's fitness; the next largest class will be those variations that are harmful with respect to fitness, and the smallest set will be those infinitesimally few dimensions of variation that can point to fitness benefits—though note, dimensions that imply fitness benefits and dimensions that imply fitness costs may often be two sides of the same coin. Assuming that the robot is able to reasonably accurately perceive potential mates along the relevant dimensions (a nontrivial but for the moment necessary assumption), robots with mating psychologies attuned to neutral dimensions to the exclusion of dimensions bearing information on harm and benefits would be outreproduced by robots with more fitness-sensitive priorities.

So, in order to discriminate between potential mates in the face of the infinite variation among them, the robot needs some means to form preferences. The word "preference" has many meanings in different contexts. For the sake of precision, here I choose to define "preferences" as parameters of functions that relate perceptions of potential mates to valenced evaluations of those mates. As such, these preferences dictate both (1) what dimensions of variation will be considered in prioritizing some potential mates over others, and (2) within those dimensions, what perceptions will be considered favorable. I will consider these psychological functions and valenced evaluations ("mate value") in the next section; here I focus on preferences themselves. We can ask at least two

important questions about these preference parameters: what is the nature of these parameters and where do they come from?

The Nature of Mate Preferences

A variety of models of mate preference have been implicit within the human mating literature. The most common of these models is likely that of mate preferences as slopes or weights. According to these models, the way that mate preferences influence the prioritization of some mates over others is by applying differential weights to dimensions of mate variation. Those dimensions that are more diagnostic of the net fitness benefits a mate offers receive greater weighting and consequently make up a greater proportion of the variation in mate value judgments; dimensions that are less diagnostic receive relatively lower weightings. Dimensions with negative polarity (e.g., aggressiveness or selfishness) can receive negative weightings. Finally, slopes can also be set such that they produce nonlinear functions, resulting in, for example, greater effects of the "negative" ends of trait dimensions compared to the "positive" end (Li et al., 2013; Long & Campbell, 2015).

Such a model of mate preferences can be inferred from Buss (1989)—perhaps the most influential study of mate preferences in the literature. Buss framed their exploration in terms of relative valuation of preferred dimensions: for instance, "females, more than males, should value attributes in potential mates such as ambition" (Buss, 1989, p. 2) and "males, more than females, will value relative youth and physical attractiveness" (Buss, 1989, p. 3). Their methods reinforce this in asking participants to both rank and rate the relative importance of different trait dimensions. Other researchers also implicitly endorse this slope model of preferences: for instance, Eastwick et al. (2019) imply such a model in proposing that the effects of preferences can only be inferred from interactions between preference values and potential mate trait values.

Although slope models of preferences are common, they are not the only existing models. Another possibility is that, rather than specifying weightings of different dimensions, preferences specify ranges of acceptable variation within dimensions. Kenrick et al. (1990) proposed such a model in a separate influential paper on mate preferences and asked participants to report the minimum and maximum percentiles they would find acceptable for a variety of characteristics potential mates might vary on. A related model is that of mate preferences as *thresholds*. According to threshold models, mate preferences dictate switch points that divide each dimension into regions of acceptable mates and regions of unacceptable mates. One prominent threshold model of mate preferences

comes from sequential aspiration model of mate choice according to Miller and Todd (1998), in which each mate preference acts as a filter that sorts undesirable mates from desirable mates, with undesirable mates being rejected and desirable mates passing on to the next filter.

Finally, a fourth computational model of mate preferences is that preferences act as ideal values to which potential mates are compared. Here mate preferences simply specify the most preferred point within the space of possible potential mates. Such a model of mate preferences is implicit within the ideal standards model of close relationships: "for example, a person's partner ideal of 'handsome and warm' represents a personally held ideal that specifies […] what the ideal would be line in an intimate relationship with the self" (Fletcher & Simpson, 2000, p. 102). Others have proposed models of preferences as ideal values as well (Conroy-Beam & Buss, 2017).

Despite long-standing attention to mate preferences within the human mating literature, the relative evidentiary standing of these alternative models of mate preferences is somewhat unclear. Although mating researchers have proposed a variety of models of preferences, these models are typically implicit, inferable only indirectly from, for instance, the methods used to study preferences. Empirical tests that compare the differential validity of different models of preferences are rare to nonexistent. The ambiguity regarding the computational implementation of mate preferences is made worse by the fact that combinations of these models are possible as well. For instance, the budget allocation approach, by Li et al. (2002), to measuring mate preferences combines both the slope and threshold models of mate preferences. For example, they suggest that "creativity might be irrelevant if a person is below threshold on attractiveness. Thus, the importance of creativity may depend on levels of other traits" (Li et al., 2002, p. 948), suggesting a relative weighting of preferred dimensions as a function of thresholds within those dimensions. Future research is needed to more explicitly explore the possible computational formats of human mate preferences.

The Origin of Mate Preferences

In addition to exploring the nature of mate preferences themselves, researchers can also ask: from where can our robot expect to get its preferences? As with all questions of behavior, this question can be answered at multiple levels. At the ultimate level, sexual selection is the most obvious source of human mate preferences (e.g., Buss, 1989). Genes interact with their environments to construct organisms and these organisms' psychologies possess

preferences. If an organism's preferences cause it to mate with partners that provide greater reproductive success, the organism will more successfully reproduce the genes responsible for its preferences. As such, preferences "for" fitness beneficial characteristics will become more common over time.

This is reasonable as a simplified model, but human mating researchers should nonetheless be aware that sexual selection theory has its own enigmas. One concerns the maintenance of preferences over time: the existence of a preference "for" a characteristic creates a selection pressure in favor of possessing that characteristic. This selection pressure should tend to winnow variation on preferred characteristics; however, a characteristic on which potential mates do not vary cannot be used for discrimination and therefore does not require a preference. Over evolutionary time, preferences should thus be self-defeating. Yet, across species, we observe the continued maintenance of variation in both preferred characteristics and preferences themselves. How can this be? This question has been referred to as the "paradox of the lek" (Rowe & Houle, 1996). There are many proposed solutions, including parasite-host coevolution (Hamilton & Zuk, 1982) and "genic capture" (Rowe & Houle, 1996). A full treatment of these issues is beyond the scope of this chapter; however, a complete model of human mating would seek evidence of these processes in the computational design of human mating psychology.

The origin of mate preferences can also be sought at the ontogenetic level. In answering questions at this level, researchers must take care to remember that mate preferences, as defined here, are not adaptations themselves but, rather, are the output of adaptations (Buss, 1989; Symons, 1989; Tooby & Cosmides, 1989). These underlying mate preference mechanisms will be sophisticated information-processing systems that capture relevant information from their environments and process it according to algorithms that calibrate the output mate preference parameters. The question then becomes: what information should our robot's mate preference psychology attend to and what mate preference parameters should it output in response?

Some have proposed that ecological factors will be relevant to these decisions. That is, in some environments, some dimension of variation may be more or less important to fitness or some regions of trait space within those dimensions may be more or less favorable. Mate preference adaptations should consequently track environmental information that pertains to this ecological variation and adjust mate preference parameters accordingly. One such proposed dimension of variation is the local prevalence of pathogens (Gangestad et al., 2006); however, some evidence does not support this specific hypothesis (Walter et al., 2020). Others have proposed and provided evidence that preference

adaptations attend to features of the organism itself: for example, mating strategy (Kenrick et al., 1990) and mate value (Buss & Shackelford, 2008).

Learning is almost certainly going to be critical to the ontogeny of mate preferences as well. That said, it is unlikely that a robot could reliably form human-like mate preferences through blank-slate, brute-force learning for at least two reasons. First, the robot could not possibly learn what to prefer by considering all possible preference dimensions because the set of possible preferences is infinite. The robot must have some a priori limits on the dimensions it will consider for learning. Second, the fitness consequences of many preferences (e.g., symmetry) are unlikely to be observable over the course of a robot's lifetime. This means that the robot will lack the feedback signals that are required for learning. For these reasons, human mate preference adaptations must be endowed with design features that privilege certain mate preferences prior to experience. Nonetheless, well-designed preference adaptations should still take advantage of experience in fine-tuning preferences or adjusting them to local ecological context. This could include individual learning on the basis of one's own mating experience (Charlot et al., 2020; Gerlach et al., 2019) as well as social/cultural learning on the basis of others' mating experience (Dugatkin & Godin, 1992; Hill & Buss, 2008). Despite the potential benefits of such learning systems, and indirect evidence for their existence, research into the computational design of the learning systems within human preference psychology is unfortunately limited.

Mate Preference Integration: Evaluating Potential Mates

Mate preferences would allow a hypothetical mate choice robot to know on which dimensions to assess its potential mates and, within those dimensions, which trait values to evaluate favorably. This is important for forming evaluations of potential mates, but preferences would not be sufficient for evaluation on their own. Selecting a mate requires translating a categorical set of potential mates into a ranking that reflects the robot's relative prioritization of those mates—relative to one another to remaining unmated or to both. This ranking could in principle be accomplished on the basis of any one mate preference; however, this is unlikely to be sufficient for fitness-beneficial mate choice because people vary at least somewhat independently across mating-relevant dimensions.

For instance, people value kindness, intelligence, and physical attractiveness in potential mates (Buss, 1989; Walter et al., 2020). A robot could order its potential mates on the basis of any one of these three dimensions—prioritizing

most heavily those mates that are most desirable in terms of either their perceived kindness, intelligence, or physical attractiveness. However, a person's kindness does not perfectly predict their intelligence or physical attractiveness, nor does a person's intelligence perfectly predict their physical attractiveness. To the extent that these dimensions are uncorrelated, mate choice that optimizes only one preference dimension will not be guaranteed to optimize any of the other relevant dimensions. That is, selecting a mate that is maximally kind may entail forgoing a mate who is more physically attractive, more intelligent, or both, and these ignored assets may have provided the robot greater fitness benefits than their chosen mate's kindness.

How, then, should the robot rank order its potential mates? The ultimate success criterion by which natural selection judges a given mate choice decision is the net fitness benefits that result from pursuing a given mate rather than others. If a mate choice robot's preference psychology is well designed, the mate preference dimensions it attends to should be observable but noisy individual reflections of this underlying, unobservable, and multivariate dimension of mate value. In order to make successful mate choices, the robot needs a means to use information from across its multiple mate preferences to form overall evaluations of potential mates that are correlated with the real mate values of those potential mates.

I will refer to this mate value evaluation process as mate preference integration. One potential rough model for this mate preference integration process is something similar to a utility function. This utility function takes perceptions of potential mates as input. Preferences act as parameters of the utility function that dictate the shape of the output as a function of the input perceptions. The output of the utility function is the perceived mate value of each of the robot's potential mates which itself must dictate, all else equal, the robot's relative interest in pursuing those mates. This utility function can be thought of as the function that is approximated when estimating preference functions (Ritchie, 1996). Depending on the nature of the utility function used, integrating mate preferences can allow the robot to use information from across its individual mate preferences but form evaluations that are more closely associated with mate value overall than any one preference dimension would allow.

Models of Mate Preference Integration

The question for mating researchers thus becomes: what is the nature of human mate preference integration functions? There are, of course, a variety of

potential models; these models are also obviously intimately linked with models of mate preferences themselves. Consequently, just as the slope model is the most common implicit computational model of mate preferences, the default assumption for the nature of mate preference integration appears to be a linear combination or weighted sum. According to this model, the mate value of potential mates is estimated as the sum of their individual trait values—presumably somehow scaled to some common metric space. However, these trait values are also weighted according to the relative importance of the different trait dimensions that contribute to the sum. This is accomplished by multiplying each potential mate's trait value by the preference parameter for that trait dimension. The result is that dimensions that are more strongly preferred apply a larger weight to trait perceptions and consequently make up a larger proportion of the variance in mate value estimates. Such a method of mate preference integration can allow all preferences to contribute to mate value estimates, and so can allow for trade-offs among dimensions. However, if mate preference parameters are tuned to between-dimension differences in contribution to fitness benefits, a linear combination can also allow those dimensions that are more important to sway decision-making more than less important dimensions. Although seldom stated explicitly as being the assumed model of mate preference integration, assumption of such a model of mate preferences can be inferred from arguments that, for instance, the effects of mate preferences are necessarily observable in the interaction between mate preferences and trait values (Fletcher et al., 2020) or in the use of Brunswick lens diagrams as models of mate choice (Buss & Schmitt, 1993).

The most common competitor models to the linear combination model are those that use threshold models of mate preferences. Of these, the most developed model is sequential aspiration model of mate choice of Miller and Todd (1998). In contrast to the continuous sum model of mate value assumed by the linear combination model, this sequential aspiration model instead proposes that mate preference integration occurs as a step function. In a sequential aspiration model of mate preference integration, mate preferences are threshold values that are used to evaluate potential mates in a sequence. Potential mates are compared to a first mate preference threshold and any potential mates who do not pass this threshold are discarded (or, alternatively, assigned the lowest possible mate value estimate). Any potential mates who pass the first mate preference threshold are then compared to a second threshold; those who do not pass this second threshold are also discarded (or assigned the second-lowest possible mate value) whereas mates who do pass the threshold are passed onto the third, and so on.

Potential mates are compared to only one mate preference threshold at each stage of this mate preference integration process and no mate preference threshold is used twice. This means that once a mate preference has been used to sort potential mates, this preference has no relevance to any future evaluations. This process could continue until a mate passes all threshold checks, no viable mates remain, or the space of potential mates has been winnowed to the smallest possible set of highest mate value options. The order of the sequence in which mate preferences are used for evaluation can be set according to at least two important considerations. The first is the cue validity of those dimensions: the degree to which a binary sorting on a given dimension is actually useful in separating high and low mate value partners. Prioritizing high cue validity dimensions for evaluations early in the mate preference integration sequence can allow for more rapid identification of high mate value partners. The second consideration is the availability of information concerning each mate preference dimension. Not all information about one's potential mates is immediately available: aspects such as physical attractiveness can be observed relatively early on in acquaintance with a potential mate whereas aspects such as parenting ability likely take longer to observe. A sequential aspiration model of mate preference integration can solve this problem by placing those mate preferences for which information can more rapidly be acquired earlier in the evaluation sequence. As a result, whereas linear combination integration either requires withholding evaluations until all information is known or making potentially misleading inferences about unknown information, sequential aspiration integration can allow for evaluation of potential mates as information about those mates becomes available.

A third class of mate preference integration models are those that assume that mate preference integration functions take the form of similarity metrics. These models of mate preference integration dovetail with ideal value models of mate preferences. Similarity metrics are functions that take as inputs two sets of values and compute a representation of how similar those two sets of values are to one another overall. In using similarity metrics in the context of mate choice, one value set will be the individual's mate preferences—acting as ideal values—and the second value set will be perceptions of a potential mate's characteristics. If the individual's preferences are set to those values that would maximize fitness benefits received from a mate, then similarity to these values can be correlated with mate value.

Among the most intuitive of these similarity metrics is the Manhattan distance. The Manhattan distance is the sum of the absolute deviation between a potential mate's traits and the evaluator's corresponding mate preferences. A

greater sum of deviations indicates lower similarity between a set of preferences and traits and, assuming preference values are well-calibrated, a lower mate value. A separate natural and closely related similarity metric is the Euclidean distance. The Euclidean distance is the square root of the sum of the squared deviations between two sets of values. If mate preferences and potential mates can be taken to represent points in a multidimensional metric space, where each dimension through this space is a separate mate preference dimension, the Euclidean distance represents the straight-line distance between a preference point and a potential mate (Conroy-Beam, 2018). A greater distance indicates a greater dissimilarity between preferences and a potential mate and therefore lower mate value. A related similarity metric is the Mahalanobis distance, which is in essence a Euclidean distance that first adjusts for correlations between preference dimensions, thereby eliminating information that is redundant across preference dimensions (Del Giudice et al., 2012). A fourth potential similarity metric is the cosine similarity. The cosine similarity is the cosine of the angle defined by a potential mate, a set of mate preferences, and the origin of the multidimensional preference space. This angle is minimized—and the cosine of this angle maximized—when a potential mate's trait point is oriented similarly with respect to the origin as is the evaluator's preference point—that is, it is high in trait value on those dimensions where preferences are high in value and low in value on those dimensions where preferences are low in value. A high cosine similarity thus can represent a higher mate value. This is numerically similar to the commonly used profile correlation metric in which the researcher computes the correlation between a set of mate preferences and a given mate's traits (Fletcher et al., 1999).

Outstanding Issues in Mate Preference Integration

Several outstanding issues remain in mapping the nature of human mate preference integration functions. Chief among them: although the literature offers an abundance of models by which human mating psychology *could* integrate human mate preferences, empirical comparisons of these alternative models are limited. Within this literature, there are two main ways by which researchers have attempted to compare the plausibility of different mate preference integration functions.

The first compares attraction to hypothetical potential mates to attraction values expected under alternative mate preference integration functions. For example, Conroy-Beam and Buss (2017) presented samples of participants with profiles of potential mates that described numerically how these mates varied

across a number of mate preference dimensions. Participants rated on a 7-point Likert scale how attracted they would be to each mate as both a long-term romantic partner and a short-term sexual partner. A variety of hypothesized mate preference integration functions were compared in their ability to predict these attraction ratings. The tested functions included the Manhattan distance, Euclidean distance, profile correlation, weighted sum, and unweighted sum. Of these, the Euclidean distance provided the best predictor of participant attraction ratings. That said, a somewhat similar study produced different results. Brandner et al. (2020) also showed participants a series of numerical profiles of hypothetical potential mates. However, rather than presenting mates one at a time for attractiveness rating, in this study participants viewed the profiles in pairs and were asked which profile in the pair they found more appealing. In this study, a weighted sum (i.e., linear combination) model performed best in predicting participant choices, with a Euclidean distance only performing second best.

A second means for comparing mate preference integration functions compares real-world romantic relationships to relationships observed in simulated mating markets. Studies using this approach generate simulated mating markets in which agents choose each other as mates according to mate values estimated by different mate preference integration functions. The nature of the agents' resulting relationships can then be compared to real-world participant relationships, with the assumption that markets based on more accurate models of mate preference integration should tend to produce more realistic relationships. Using this approach, Conroy-Beam (2018) found that mate choice according to a Euclidean integration function produces a signature pattern of effects that is not well reproduced by alternative functions. Specifically, agents select mates that strongly embody their preferences overall, but agents that are themselves higher in mate value according to Euclidean calculations tend to (1) better fulfill their own mate preferences, (2) set higher standards, and (3) pair with higher mate value partners. This same pattern of effects was observed in samples of human relationships and is quantitatively most similar to the patterns produced in simulations of Euclidean mate choice as opposed to other integration functions. Furthermore, this pattern—and its unique similarity to Euclidean models of mate choice—replicates in a cross-cultural sample with participants from 45 countries around the world (Conroy-Beam et al., 2019). So overall, similarity functions appear to perform well as models of human mate preference integration, in particular, a Euclidean distance function. However, the existing literature is small and has somewhat conflicting results.

A second outstanding issue concerns the available models of mate preference

integration. The models I have reviewed here are the ones that are prominent—explicitly or implicitly—within the prior literature on human mate choice. But these are not the only possible models and new models should be developed and considered as well. One potentially fruitful avenue for the development of new models would be combining the models I have outlined here. For instance, linear combination models and similarity metric models could be combined to create weighted similarity functions. Such functions could still compute mate value as the similarity between a mate and a set of preferences but could weigh more important dimensions more heavily in computing that overall similarity. Each preference dimension would contribute two parameters to the preference integration function: one parameter that reflects the relative importance of different mate preference dimensions and a second parameter that specifies the ideal value within each dimension. These and other combinations are as yet untested within the small preference integration literature and could offer models that perform better than their individual components.

Finally, a third outstanding issue that researchers should keep in mind is that human mate preference integration functions need not be singular. Human mating psychology could in principle contain a variety of integration functions that are deployed conditionally. This means that mate preference integration functions could vary across contexts, across time, across people, across cultures, or across stages of the mate choice process. For instance, it could be that people who need to make mating decisions more rapidly opt to use sequential aspiration integration whereas those who have more of the luxury of time opt for similarity functions or linear combinations. In further exploring the nature of human mate preference integration, researchers should remain open-minded to the possibility of variability in the nature of mate preference integration functions.

Mate Choice Algorithms: Choosing a Mate

At this stage, we can in principle construct a robot that knows on what dimensions to assess its potential mates and is capable of integrating information on potential mates across dimensions into an overall summary of mate value, hopefully correlated with the fitness benefits pursuing a mate would provide. Now the robot needs to use these summary evaluations to actually pursue and choose a mate. The problem here is that mating markets inherently pose a number of constraints that make the robot's decision problem more complex than the problems faced in the prior two stages (Conroy-Beam & Buss, 2020). The first such constraint is the issue of *availability*: there is no guarantee that the robot's ideal partner will exist in their local mating market—in fact, there is

nearly a guarantee that they will not. The robot's task is thus not simply to find their ideal partner but rather to acquire as high a mate value partner as it is able. This task is made more difficult by the second constraint: *competition*. Human pair-bonding imposes a relatively sharp limit on the number of romantic partners a person holds at any one time. This limit is very near one: although historically most societies have allowed some degree of polygyny, allowing men to marry multiple women, even within these societies the majority of marriages have historically been monogamous (White et al., 1988). This means that a potential mate that pairs with a rival can be effectively removed from the mating market; the robot is limited to choosing among mates that are either single or capable of being poached from their partners. The final constraint imposes the most complications of all: human mate choice is generally *mutual*. Whereas in most species mating can be adequately described as members of one sex choosing members of the other, in humans both partners—and often, to varying degrees, their families and friends—must mutually agree to enter a mating relationship with one another (Stewart-Williams & Thomas, 2013). This means that the robot cannot stubbornly pursue only those partners that appear highest in mate value to it; it must also consider the interests of its potential partners, its rivals, and other influential agents and guide its mate pursuit toward appealing partners with whom it can establish mutual attraction.

The end result of these constraints is a mating market that exists as a highly interconnected social system wherein the choices available to the mate choice robot depend on the choices made by each of their mating rivals as well as each of their potential mates. For example, a high mate value rival rejected by their first-choice partner may choose to pursue the robot's first choice partner, forcing the robot to switch to their second-choice partner—a change in the robot's own mate pursuit forced entirely by the decisions of third parties. Navigating these scenarios requires a nimble decision-making psychology that deploys algorithms capable of dynamically adjusting the robot's mate pursuit in response to the ever-shifting state of the robot's mating market. This psychology also must take care to balance two competing demands: maximizing the mate value of the robot's ultimately chosen partner while also minimizing search costs en route to this choice. All else equal, a higher mate value partner obviously represents a better mate choice than a lower mate value partner. However, time and energy available for mate search is finite and resources spent doggedly pursuing unrealistic options could more profitably be spent pursuing partners more likely to be mutually interested. Selection is likely to have historically favored the evolution of mate choice algorithms that directed mate search to high value partners but still made prudent use of limited mate search resources.

Mate Choice Algorithms

Precisely which decision algorithms could a mate choice robot use to solve the many problems posed by human mating markets? Available models of human mate choice algorithms are few in number. Three algorithms in particular, however, have received some attention in the mating literature. The first is the model of assortative mating by Kalick and Hamilton (1986). This model was proposed to explain the commonly observed correlation in physical attractiveness between mated partners: attractive people tend to pair with attractive partners. Within the field of social psychology, a dominant explanation for this phenomenon has historically been a preference for self-similar partners. Kalick and Hamilton's model tested the sufficiency of an alternative hypothesis: people prefer physically attractive partners, this preference gives attractive people more power to choose the partners they desire, and physically attractive people use this power to pick more attractive partners.

The model was intended as a stylized sketch of a possible mate choice algorithm; nonetheless, despite its simplicity, it does expose a means by which human mating psychology could solve real-world mating problems. Their model assumes a population of agents, each of whom possesses a random physical attractiveness value. Although Kalick and Hamilton were focused specifically on the issue of physical attractiveness, "attractiveness" in their model could easily be substituted for overall mate value. Agents in this model go on dates with randomly chosen partners and on each date decide whether or not to commit for life to their date partner. The commitment decision is made on the basis of a weighted coin flip, where the probability of an affirmative decision is proportional to two things: the attractiveness of the agent's date partner and the number of unsuccessful dates the agent has had already. In this way, the decision process implied by this model manages to balance both pursuing high value partners and minimizing search costs. The model additionally incorporates the mutual nature of choice in that both agents need to make mutual offers of commitment to enter a relationship. If such a mutual agreement is reached, both agents exit the mating market together; if either agent declines to commit to their date partner, both agents reenter the mating market and continue dating until they find a partner.

A second prominent model of human mate choice algorithms is actually a class of similar models proposed in slightly different forms by Peter Todd and colleagues (e.g., Todd et al., 2005; Todd & Miller, 1999). A recurrent feature of these models is learned aspiration thresholds that guide mate choice and are calibrated based on experience. For example, an early version of this model—

with features common to later elaborations—divides mate choice into two phases. In an early "adolescence" phase, agents go on dates with random partners similarly to the model of Kalick and Hamilton (1986). On these dates, agents make nonbinding expressions of interest based on mate value aspiration thresholds. These aspiration thresholds are initially set to arbitrary values and each agent expresses interest in any potential mate whose perceived mate value exceeds the current value of their threshold. The agents then update the value their thresholds based on the result of their dates. If an agent receives an expression of interest from an agent whose mate value was above their current threshold, this suggests the agent could afford to be more selective; consequently, the agent adjusts their threshold upward slightly in the direction of the mate value of their date. When an agent is rejected by a date with a mate value below their threshold, this suggests the agent has been too ambitious and so they reduce their threshold toward their date's mate value. If this learning process proceeds for long enough, agents can tune their threshold to high value partners who are likely to reciprocally pursue the agent, thereby balancing the need to maximize partner value while also minimizing search costs. Afterward, agents exit the adolescence phase and begin real mate choice. Here agents continue going on random dates; however, now they use their aspiration threshold to make real offers of commitment. Agents offer commitment to any date partner that exceeds their aspiration threshold; if their partner reciprocates their commitment, both agents exit the mating market together. By following this aspiration threshold algorithm, agents can accomplish successful mutual mate choice sensitive to both their own mate preferences and the preferences of others.

A third potential model of human mate choice comes from economics: the Gale-Shapley algorithm (Gale & Shapley, 1962). While this algorithm has been applied to model mate choice (Hitsch et al., 2006; Xie et al., 2015), it was originally developed as a solution to the more general problem of "two-sided matching": that is, any problem, mate choice included, where items from two sets must be sorted into pairs based on the preferences of individuals. In a mate choice context, these two sets are generally males and females. In the first step of this algorithm, each male approaches and offers commitment to the female who is highest in mate value to him. This algorithm thus differs from the prior two algorithms in that mate approach is deterministic: rather than going on random dates, contacts between potential mates are based on preferences. After males approach their most preferred partners, females select among their suitors: each female temporarily pairs with the suitor that is highest in mate value to her and permanently rejects all others. Rejected males then make a new round of

offers, each pursuing the female that is highest in mate value to them but who has not yet rejected him. Females then make another round of choices, with each female comparing her current temporary partner to her suitors. If no suitor is higher in mate value than her partner, she rejects all of the suitors; however, if any of the suitors is higher in mate value than her partner, she pairs with that suitor and rejects her former partner along with all of the lower mate value suitors. This pursuit and choice cycle repeats until all agents have found partners. A potential advantage of this algorithm as a mate choice algorithm is that, in a population of individuals who choose mates according to the Gale-Shapley algorithm, all individuals are guaranteed to find partners and their pairs will be "stable" in the sense that no individual would prefer to pair with someone who would also prefer them in return. However, a noteworthy potential limitation of this model is that although it does incorporate mutual mate choice, it assumes mate choice is inherently asymmetric: males approach partners and females choose among their suitors; females have no power to actively approach partners high in mate value to them. As a result, Gale-Shapley pairings tend to better optimize male mate preferences than female mate preferences. This assumption is not likely to typify human mate choice (Stewart-Williams & Thomas, 2013).

These models represent just three prominent example models from the literature on modeling mate choice. Although three models these have received much attention, other interesting models exist as well. For instance, French and Kus (2008) proposed a model called KAMA in which mate choice is regulated by a computational "temperature" value that controls how motivated an individual is to find a partner and could be considered a computational representation of mating effort. Smaldino and Schank (2012) proposed a model similar to that of Kalick and Hamilton (1986) but which incorporates more realistic spatial constraints.

All these models propose a mixture of unique and borrowed features, each of which may be strengths or weaknesses in terms of accurately modeling human mate choice algorithms. Empirical comparisons of alternative mate choice algorithms are rare. Within these rare comparisons, the most common method of evaluating proposed mate choice algorithms is testing their ability to reproduce population-level mating-related characteristics such as degrees of assortative mating (Hitsch et al., 2006; Kalick & Hamilton, 1986) or hazard rates of marriage as a function of age (Todd et al., 2005). These are important criteria as they do describe real human mating phenomena which any accurate model of human mate choice should be able to reproduce. Nevertheless, that so many different models, that differ so dramatically in their underlying mechanics, are

all capable of reasonably approximating these population-level characteristics suggests that more nuanced and fine-grained comparisons will be necessary to advance our understanding of human mate choice algorithms. This is likely to come from empirical paradigms that, rather than studying mate choice at the population aggregate level, compare the real-world mate choice behavior of individuals to behavior expected under hypothesized mate choice algorithms (e.g., see Beckage et al., 2009).

Conclusions and Future Directions

Mate choice is among the most important decisions that confronts a sexually reproducing species like our own. But human mate choice takes place in the context of dynamic and interconnected social systems that render mating markets challenging to understand with unaided intuition alone. Computational modeling provides invaluable tools for clearly and transparently making predictions about such complex systems. And although the state of computational modeling of human mate choice is still in its infancy, this small literature already offers several models that have provided insight into real-world mating phenomena and offer a platform upon which future research can build to more thoroughly detail the computational design of human mating psychology.

I have focused here on computational models of three elements of human mate choice: mate preferences, mate evaluation, and actual mate choices. These examples were intended to be illustrative rather than exhaustive and no model presented here should be taken to be the final word on the nature of human mating psychology. Future research must expand the models available for describing mating psychology pertaining to each of these phases. Computational models also must extend beyond these three stages to other important stages of human mating. Two of these deserve some special mention.

The first is the nature of mate search. In all of the models discussed here, the mate choice robot simply knows who all of its potential mates are and what they are like. However, this cannot be taken for granted. For one, human mating markets exist within a metapopulation of different mating markets and people can and do move between different markets in search of better mating opportunities (Cashdan & Gaulin, 2016). These markets will inevitably differ from one another in mating relevant ways. For instance, some markets will be lush with potential mates (e.g., dense urban environments) whereas others will have scarcer mating opportunities (e.g., more isolated, rural areas). Different markets may therefore offer different combinations of challenges that might be more or less appealing to individual mate seekers: for example, rural markets

may offer less availability but less competition, whereas urban markets may offer more availability but more competition.

Furthermore, not all individuals necessarily search their local markets to the same degree: high mating effort individuals might choose to search their mating markets relatively exhaustively whereas low mating effort individuals might prefer to reserve that time and energy for other tasks. Two individuals who share the same objective mating market may therefore experience quite different effective mating markets depending on the mate search decisions they make. Models of decision making at the level of the mating market and its consequences for individual mating markets will likely be essential for fully describing human mating decisions.

Additionally, even within a mating market, not all individuals are necessarily considered potential mates. For instance, for most individuals, members of one's own sex are automatically ruled out as potential partners for the obvious reason that reproduction requires heterosexual mating. Similarly, pre- or postreproductive individuals are likely ruled out by individuals in their reproductive years. Future research must build models of this decision process by which individuals determine who qualifies as a potential mate to begin with. This will likely dovetail with research on "deal-breakers" in mate choice (Jonason et al., 2015) as well as research suggesting that avoiding mates with negative qualities shapes mate choice more than does pursuit of mates with positive qualities (Long & Campbell, 2015).

Finally, in all the models considered here, information on potential mates comes veridically and for free. However, in the real world, perception is inherently noisy and potential mates are incentivized to deceive by embellishing their positive qualities and concealing their negative qualities (Haselton et al., 2005). Real mate perception likely therefore requires investing limited time and energy into harvesting observations of potential mates—either directly or indirectly through reputational information—and the application of statistical reasoning mechanisms that can form perceptions of potential mates in spite of the inherent noisiness of incoming information. In the examples discussed here, I took for granted that the fictional mate choice robot could access accurate assessments of potential mates on any relevant dimension. But in reality, human mating psychology must have sophisticated mate perception adaptations designed to solve the problems inherent to forming such assessments. The design of this mate perception psychology, and its implications for mate assessment and evaluation, will be an essential component of more complete computational models of human mating psychology.

A second important extension of computational models of mating will be to

move models beyond the mate choice process and into the psychology responsible for regulating the subsequent relationships mate choice creates. Successfully regulating a romantic relationship poses a number of problems: encouraging beneficial behavior from your partner and discouraging bad behavior, maintaining good relationships but dissolving bad relationships, switching to better relationships when they are available but preventing your partner from doing the same, and supporting your partner toward accomplishing shared goals but directing them away from selfish endeavors. Not all these problems can be solved at the same time, nor are all problems equally worth solving at any given time. Successfully navigating romantic relationships will therefore require information-processing mechanisms that are able to decide which problems require priority. And solving each of these problems will require specialized psychological adaptations that can capture information relevant to those specific problems and use it to mobilize context-specific responses. The problems an individual will encounter in the course of their romantic relationship will likely be intimately linked to their mate choice and so the ultimate future direction for models of mate choice will be to build upon them to construct complete models of the entire lifespan of human romantic relationships.

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CHAPTER
7

The Logic of Physical Attractiveness: What People Find Attractive, When, and Why

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Abstract

Attractiveness is a perception produced by psychological mechanisms in the mind of the perceiver. Understanding attractiveness therefore requires an understanding of these mechanisms. This includes the selection pressures that shaped them and their resulting information-processing architecture, including the cues they attend to and the context-dependent manner in which they respond to those cues. We review a diverse array of fitness-relevant cues along with evidence that the human mind processes these cues when making attractiveness judgments. For some of these cues, there is unequivocal evidence that the cue influences attractiveness judgments, but exactly *why* attractiveness-assessment mechanisms track that cue is an area of current debate. Another area of active inquiry is *when* these cues influence attractiveness judgments: because the fitness costs and benefits associated with these cues would have varied across contexts, selection should have shaped attractiveness-assessment mechanisms to be sensitive to contextual variables. As a consequence of this context-sensitive design, these mechanisms, despite being universal, should produce attractiveness assessments that vary systematically and predictably across contexts. We review evidence indicating that this is how human perception of attractiveness works, and highlight the need for more comprehensive and systematic investigations into contextual variation in human standards of attractiveness. We conclude by identifying limitations on existing evolutionary research on attractiveness, and provide concrete suggestions for how future work can address these issues.

Key Words: physical attractiveness, evolutionary psychology, mate

preferences, waist-to-hip ratio, fluctuating asymmetry

Attractiveness is not an inherent property of the entity being perceived; it is a perception produced by psychological mechanisms in the mind of the perceiver. Understanding attractiveness therefore requires an understanding of these mechanisms. This includes their causal origins—the selection pressures that shaped them—and the resulting design of their information-processing architecture, including the specific cues they attend to and their sensitivity to contextual variables.

In this chapter, we first identify what attractiveness is and what perceptions of it do. The motivational consequences of perceiving another individual as attractive provide key insight into why evolution by natural selection would have shaped these mechanisms in the first place: to guide people toward fitness-enhancing selection of relationship partners.

We review a diverse array of these fitness-relevant cues and the empirical evidence demonstrating that the human mind regulates its perceptions of potential mates' attractiveness in response to them. For some cues, it is clear *whether* they influence perceptions of attractiveness, but the precise evolutionary reason *why* attractiveness-assessment mechanisms track that cue is an area of current debate. Another area of active inquiry is *when* these cues influence perceptions of attractiveness—the fitness costs and benefits of the traits indicated by the cues would have varied across contexts, so selection should have shaped attractiveness-assessment mechanisms to be sensitive to these contextual variables. Because of this context-sensitive design, these mechanisms should produce attractiveness assessments that vary systematically and predictably across different contexts. We review evidence suggesting that this is how these mechanisms operate, and highlight the need for more comprehensive and systematic investigations into cross-context variation in human standards of attractiveness.

We then briefly contextualize these empirical findings and theoretical ideas in the broader landscape of interpersonal attraction. This chapter focuses on the perception of attractiveness in response to cues that are (1) morphological, (2) visually observable, and (3) of fitness relevance for mating relationships. Humans' broader psychology of interpersonal attraction also includes cues that are dynamic (i.e., movement-based), detectable via nonvisual modalities (e.g., olfaction, audition), and relevant to nonmating relationships (e.g., kin-based relationships, friendships, coalitions). Although it is beyond the scope of the current chapter to cover this entire landscape, the principles and evolutionary

logic that we outline here apply across different classes of cues, across the different perceptual modalities by which they are detected, and across human relationship types.

Finally, we conclude by identifying significant limitations on existing evolutionary research on attractiveness, and provide concrete suggestions for future work to address these issues.

Attractiveness as Perception

Attractiveness is commonly attributed to the perceived entity itself: "that flower is beautiful," "that man is unattractive." However, attractiveness is not a property of the object being perceived, but rather is a perception produced by psychological mechanisms in the mind of the perceiver.

This important distinction is illustrated well by humans' aversion to—and houseflies' affinity for—the volatized chemical compounds emitted from feces. When olfactory receptor cells bind to these chemical compounds, they initiate a relay of electrical and chemical messages that results—for humans—in the perception of an unpleasant smell, a feeling of disgust, and avoidance of the source of the odorants (Rozin & Fallon, 1987). For flies (e.g., the common housefly, *Musca domestica*, or its close relative *Musca sorbens*), the same chemical compounds evoke a diametric set of motivational and behavioral outcomes (Robinson et al., 2020). The fact that feces can be both attractive (to houseflies) and unattractive (to humans) underscores that attractiveness is not a property of the perceived entity but rather a perception produced by mechanisms in the mind of the perceiver. Understanding attractiveness therefore requires an understanding of these mechanisms.

First, we must understand their causal origins. Because evolution by natural selection is the only known causal process capable of producing complex organic mechanisms, an understanding of these mechanisms requires an understanding of the selective pressures that shaped them.

The Selective Origins of Attractiveness-Assessment Mechanisms

Our example of feces, houseflies, and humans also illustrates *why* selection fashioned psychological mechanisms that produce perceptions of attractiveness. Imagine a world in which houseflies do *not* exhibit any affinity for feces. Let us introduce into that world a "mutant" housefly that is equipped with cognitive (i.e., information-processing) machinery that, in response to detecting cues to presence of feces, motivates approach behavior toward their source. Because feces are a valuable source of nutrition for housefly larval development—

because feces *helped* houseflies solve an adaptive problem recurrently faced during their species' evolution (Robinson et al., 2020)—mutant houseflies would enjoy greater fitness than their counterparts who were not attracted to feces. This greater fitness of the mutant housefly means that the proportion of houseflies with this cognitive machinery would increase in the population in each subsequent generation until the entire population consisted of mutant houseflies: the information-processing mechanisms responsible for detecting cues to feces and motivating approach would become a universal component of housefly nature.

For humans, on the other hand, feces are a source of disease; they *cause* an adaptive problem (Cosmides & Tooby, 1997). Consequently, we should expect humans to possess psychological mechanisms to detect and process cues to the presence of feces, but with design features that are opposite to those observed in flies. Ancestral humans who possessed psychological mechanisms that responded to cues to feces with subjective states motivating avoidance behavior would have experienced greater fitness than individuals who lacked these mechanisms.

This is why selection shaped mechanisms in both houseflies and humans to detect volatilized chemical compounds that cue the presence of feces, but with different design features: in houseflies, the mechanism motivates approach in response to cues to feces, whereas humans' mechanism produces subjective states, such as repulsion and a feeling of disgust, that instead motivate avoidance (Cosmides & Tooby, 1997).

The same evolutionary logic applies to the information-processing mechanisms responsible for perceiving another individual as attractive. Ancestral humans who possessed psychological mechanisms that (1) attended to cues in a potential mate that were predictive of positive fitness consequences of mating with that individual and (2) generated preferences for mates exhibiting these cues would have outreproduced their counterparts who lacked such mechanisms. Because the individuals with these psychological mechanisms would have enjoyed greater fitness, the proportion of the population that possessed this cognitive machinery would have increased iteratively across generations until these information-processing mechanisms became a universal component of human nature.

The selective origins of these mechanisms have key implications for their information-processing design. Selection shaped these mechanisms to attend to cues in a potential mate that were ancestrally predictive of the fitness consequences of mating with that individual (henceforth, the cue's *fitness value*). This is the first key design feature of attractiveness-assessment mechanisms:

selection shaped them to attend and respond to cues that were relevant to reproductive fitness.

However, the fitness value of a cue would have varied across contexts. For example, the fitness value of a cue to immediate fertility is greater in the context of short-term mating than in the context of long-term mating; a conspecific's immediate fertility may be paramount for reaping fitness benefits from a single act of sexual intercourse, but largely irrelevant to the fitness consequences of selecting that individual as a long-term mate. The opposite is true of cues to future reproductive potential; cues to future reproductive potential may be paramount in long-term mating but largely irrelevant to short-term mating (see Goetz et al., 2012, for dozens of cues hypothesized to predict different fitness consequences in short-term vs. long-term mating). The broader point is that, because the fitness value of a cue systematically depends on specific contextual variables, selection should have shaped attractiveness-assessment mechanisms to be sensitive to these contextual variables. This is important because it means that, despite the universality of these psychological mechanisms, they should produce systematic variation in what people find attractive across contexts, including across cultures.

Whether, *Why*, and *When*: Three Interrelated but Distinct Questions

In the following sections, we discuss how attractiveness-assessment mechanisms regulate attractiveness perceptions in response to (1) cues ancestrally predictive of the fitness consequences of mating with a particular individual and (2) contextual variables that shift the fitness value of those cues.

We approach this task in a manner that differs from previous literature. Previous work in this domain (e.g., Sugiyama, 2015) has interwoven evidence that the mind tracks a cue (which answers the question of *whether* attractiveness-assessment mechanisms track that cue) with proposed explanations for *why* they track that cue, with documented or hypothesized variation in how the mechanism responds to that cue across contexts (*when*). Our primary reason for addressing these three issues separately is that existing answers to these three questions have very different statuses. In some cases, decades of empirical research have demonstrated robust effects of a cue on perceptions of attractiveness, but uncertainty remains about which existing hypothesis, if any, correctly accounts for why this cue is important. These divergent statuses of *whether* and *why* may reflect an underspecification of hypotheses. Later, we discuss this issue at greater

length and make specific recommendations for how to resolve it. Nonetheless, the current state of knowledge is such that, for many cues, answers to *whether* attractiveness-assessment mechanisms track them and *why* they do are characterized by very different levels of certainty. It therefore makes sense to address these questions separately.

Why Specific Cues Should Influence Attractiveness, and Whether They Do

For each cue discussed below, we outline *why* selection might have shaped psychological mechanisms to attend to that cue: what fitness-related trait or traits appear to be linked to that phenotypic cue? We attempt to highlight, where appropriate, the tentative nature of claims about the fitness implications of the cue. In some cases, robust empirical links exist between cues and fitness-relevant outcomes. In other cases, the link between a cue and fitness-relevant outcomes may only be hypothesized, or the cue may exhibit a tenuous empirical relationship to a fitness-relevant outcome—or doubt has been cast by recent work on a link that was once regarded as robust.

After addressing the *why*, we address *whether* attractiveness-assessment mechanisms track these cues. By and large, the corpus of empirical literature indicates that attractiveness-assessment mechanisms do track these cues. However, recent developments that have occurred in association with the movement in psychological science toward more open, preregistered science and the publication of null results suggest that some of these links may be less reliable and weaker than once thought. We attempt to balance discussion between the accumulated corpus of literature with recent concerns about some historically influential claims.

SYMMETRY

Many developmental programs are designed to produce bilaterally symmetrical features: right and left eyes that are the same size and shape—and at the same height on the face, a nose that aligns with the midline of the face and has equal-sized right and left sides, and legs of the same length. Deviations from bilateral symmetry in these features have been hypothesized to cue developmental instability, reflect mutational load or deleterious homozygosity, and be associated with lower levels of fitness (see Van Dongen, 2006, 2016, for review).

Links between symmetry and fitness-related outcomes have been documented in both nonhuman animals and humans. Research on nonhuman animals has documented links between symmetry and a diverse range of these outcomes,

from growth and survival to fecundity and mating success (see Van Dongen, 2006). Research on humans has reported associations between symmetry and similarly diverse fitness-linked variables. For example, Waynforth (1998) showed that greater symmetry was associated with lower morbidity and greater fecundity among Mayan men in rural Belize. In WEIRD (Western, educated, industrialized, rich, and democratic) populations with lower levels of exposure to pathogens, resource scarcity, and other environmental stressors, some of the associations between symmetry and health may be attenuated or absent (e.g., see Pound et al., 2014). In these environments, symmetry nonetheless appears to be positively associated with IQ (Pound et al., 2014) and meta-analyses indicate a small but positive correlation between symmetry and general mental ability (range for estimate of population-level correlation: 0.12–0.20, see Banks et al., 2010). Low levels of symmetry have also been linked to the development of schizophrenia, and, among schizophrenics, those who exhibit greater asymmetry experience earlier onset of the disease and suffer from greater disease severity (Markow & Wandler, 1986).

The reliability and robustness of these links, however, is an area of active debate. Studies investigating associations between symmetry and fitness in nonhuman taxa have exhibited a great deal of heterogeneity, and, in humans, the strength of association between symmetry and various fitness-related outcomes has differed substantially across studies. Although the mean documented effect size is approximately 0.2, study-specific effect sizes have ranged widely—from *negative* 0.2 to 1.0—and have been inversely related to sample size. These issues raise concerns about publication bias and the reproducibility of these reported symmetry–fitness links (see Van Dongen & Gangestad, 2011; Van Dongen, 2016). Nonetheless, available evidence suggests that, at least in some cases, symmetry can cue genetic quality and exposure to environmental stressors during development (Van Dongen, 2016). For example, symmetry reliably tracks developmental stability in cases of substantial ontogenetic insult (e.g., Bots et al., 2014; Woolf & Gianas, 1977), and the harsher ecological conditions experienced by foraging populations are associated with higher mean population-level asymmetry than that observed in WEIRD populations (Gray & Marlowe, 2002). This may be an important piece of the puzzle: variation in symmetry may not reliably track individual quality in WEIRD societies, but it may reliably track individual quality in environments that more closely approximate the conditions in which our species evolved. Future research is needed to map the conditions in which symmetry reliably predicts fitness-relevant outcomes, but if the observed symmetry–fitness associations held under ancestral conditions, then selection should have shaped attractiveness-

assessment mechanisms to attend to symmetry.

Numerous studies report findings consistent with this hypothesis. People perceive more symmetrical faces—both male and female—to be more attractive (e.g., Rhodes, 2006). People with more symmetrical bodies—from college students to villagers in Dominica—are rated as more attractive (Brown et al., 2008; Hume & Montgomerie, 2001; Thornhill & Gangestad, 1994). Individuals with more symmetrical bodies report having sex earlier in life (Thornhill & Gangestad, 1994) and a greater number of sexual affair partners (Gangestad & Thornhill, 1997), copulations with mated individuals (Gangestad & Thornhill, 1997), and lifetime sexual partners (Thornhill & Gangestad, 1994). Van Dongen and Gangestad's (2011) meta-analysis of nearly one hundred studies involving close to 50,000 participants revealed robust, though small, statistical associations (1) between symmetry and multiple broad categories of fitness-related outcomes, from health to psychological maladaptation, and (2) between symmetry and perceptions of attractiveness.

These findings suggest that the human mind possesses psychological mechanisms to track symmetry and regulate perceptions of attractiveness in response to it. However, several important concerns have been raised in recent literature about the reproducibility of reported symmetry–attractiveness links. First, multiple studies have found no such effect (e.g., Jones & Jaeger, 2019; Weiss et al., 2020). Second, symmetry–attractiveness relationships appear to be highly sensitive to the method and measurements employed. Compared to studies that measure naturally occurring variation in symmetry, studies that manipulate symmetry are statistically more powerful and thereby more likely to detect an effect—but they also may break up naturally occurring associations between symmetry and other hypothesized cues to individual quality (Van Dongen, 2016), which undermines the ecological validity of any reported effects. The effect of symmetry on social perceptions (e.g., attractiveness) also appears to be largely contingent on how symmetry is scored. Studies using the scoring method of Horizontal Fluctuating Asymmetry (HFA) appear to disproportionately report associations between symmetry and attractiveness (see Weiss et al., 2020). This raises flags because the other traditional scoring method —Horizontal Angular Asymmetry (HAA)—is arguably the purer measure of symmetry; unlike HFA, it is not sensitive to extrinsic factors (e.g., head roll or yaw, see Weiss et al., 2020). Even more strongly, Weiss et al. (2020) have shown that HFA may capture *only* these extrinsic factors and not be linked to intrinsic asymmetry at all. HAA is not free of issues, either, however. Of four distinct forms of intrinsic facial asymmetry, HAA fails to capture significant variance on two of these dimensions (see Weiss et al., 2020)—which calls into question any

HAA-based claims that perceptions of attractiveness are *not* related to symmetry.

Clearly, superior measures of symmetry are needed, but it is not clear exactly what such a superior measure will look like—or, for that matter, whether measuring a single type of symmetry is appropriate. Weiss et al. (2020) have provided evidence that there are at least four distinct types of asymmetry in the face alone, and that the human mind tracks these different types of asymmetry independently. These findings raise concerns about using a single, composite measure of symmetry, as distinct types of symmetry may cue distinct information and have different effects on attractiveness perceptions. By using a single composite measure, these effects could be muddled or lost altogether: when Weiss et al. (2020) created an aggregate measure of facial asymmetry based on the four types of symmetry they identified, the aggregate measure failed to capture the effects that were exerted by the individual types independently.

In sum, future work is needed to more conclusively test the hypothesis that symmetry is a fitness-relevant cue that influences perceptions of attractiveness. A key goal of future research should be to more clearly establish the precise conditions in which symmetry reliably cues developmental stability or other fitness-relevant variables. This information will be essential for researchers to generate theoretically anchored hypotheses about why, when, and how humans' attractiveness-assessment mechanisms track symmetry in the human phenotype.

WAIST-TO-HIP RATIO

The ratio of a woman's waist circumference to her hip circumference (waist-to-hip ratio, or WHR) has been hypothesized to be linked to myriad fitness-related variables—as many as forty-two, according to Bovet's systematic review (see Bovet, 2019, fig. 1, panel B). As Bovet (2019) points out, robust empirical links to WHR exist for fewer than half of these fitness-related outcomes, many of the fitness-related outcomes that are linked to high WHR are evolutionarily novel and pertain only to WEIRD societies (Eaton et al., 1997), and links between WHR and some of these outcomes have been documented predominantly among individuals over sixty—well beyond when most reproductively relevant mate choices would have occurred in ancestral conditions. These observations are valuable for ruling out specific hypotheses. However, they should not be interpreted to mean that WHR does not cue important fitness-related information: the best available evidence suggests that it does.

WHR appears to be a reliable cue to *parity*. The allocation of gluteofemoral fat deposits during pregnancy and lactation, coupled with the deposition of fat on

the abdomen after the postpartum period, increases waist circumference relative to hip circumference. This results in WHR increasing with number of previous pregnancies, an observation that has been documented among human populations on all inhabited continents and in both WEIRD and nonindustrial societies (see, e.g., Butovskaya et al., 2017; Lassek & Gaulin; 2006).

Parity would have been a fitness-critical variable for two different reasons. First, due to women's finite reproductive resources, the *number* of future children that a woman can bear is inversely related to the number she has already borne. Second, the *quality* of future descendants is also influenced by parity: high parity is associated with both lower birthweight (e.g., Kiely et al., 1986) and lower IQ (i.e., later-born children have lower IQ than first-born children; see Rohrer et al., 2015), as well as with a reduced capacity to buffer fetal development against environmental stressors (Merklinger-Gruchala et al., 2017).

Future work is needed to further assess the plausibility of the (at least) seventeen other hypotheses for why selection should have shaped attractiveness-assessment mechanisms in men to attend to women's WHR (see Bovet, 2019). However, because of (1) the robust links between WHR and parity and (2) the relevance of parity for reproductive fitness, selection should have shaped male psychological mechanisms to attend to women's WHR when producing attractiveness judgments.

A multitude of empirical studies employing diverse methods and drawing on numerous sources of data have shown that women's WHR does indeed influence men's perception of their attractiveness. This body of research has included studies employing methods ranging from simple line drawings (e.g., Singh, 1993a) to 3D body scans (Brown et al., 2008) to brain activity (e.g., Platek & Singh, 2010). It has also included the use of archival data, such as the WHRs of Miss America winners and Playboy playmates in the last century (Bovet & Raymond, 2015; Singh, 1993a), as well as the WHR of the idealized woman as depicted in Western artwork over the last 2,500 years (Bovet & Raymond, 2015). It also has included research demonstrating that congenitally blind men without any previous visual experience prefer a low WHR when assessing female body shape through touch—a preference that their sighted counterparts also exhibit (Karremans et al., 2010). So many studies have documented the influence of women's WHR on men's perceptions of their attractiveness that some authors refer to the number of studies that have *not* found such preferences: "Only three studies report no effect of WHR on attractiveness" (Sugiyama, 2015, p. 50). In these rare cases where no male preference for a specific female WHR was observed, the studies' stimulus sets included a very small number of stimuli, conflated WHR with other variables such as body weight, or both (see

Sugiyama, 2015). Follow-up studies (e.g., Sugiyama, 2004b; Tovée et al., 2006) that addressed these confounds showed that men's preferences for specific WHR values become clear when WHR is disentangled from confounds such as weight or body fat. Subsequently, Singh et al. (2010) cross-culturally demonstrated that WHR influences perceptions of attractiveness independent of body weight or body mass index (BMI). In their research, Singh and colleagues used stimuli that manipulated WHR but not BMI: they used pre- and postoperative photographs of women who had undergone micrograft surgery to remove fat from the abdomen and deposit it in the buttocks. Raters from four distinct cultures—Bakossiland in Cameroon, Komodo Island in Indonesia, New Zealand, and Samoa—judged the postoperative photos to be more attractive. In addition to these within-woman shifts in attractiveness predicted by their reduced WHR, between-woman variation in WHR also predicted perceptions of attractiveness in all four cultures. Finally, Platek and Singh (2010) showed that when men viewed the photos, the changes in WHR associated with the postoperative photos were associated with the activation of the anterior cingulate cortex, a region of the brain involved in reward and decision-making.

In short, there is an abundance of evidence that the male mind tracks women's WHR. Nonetheless, further work is needed to pin down precisely *why* selection shaped male psychological mechanisms to attend to women's WHR. The parity hypothesis appears to be the leading hypothesis for why men's attractiveness-assessment mechanisms attend to women's WHR. However, other hypotheses may overlap with this hypothesis (e.g., the hypothesis that WHR cues the quantity and availability of "reproductive fat"—see Singh, 1993b, and Bovet, 2019, for review), and yet others propose alternative, or additional, selection pressures for the evolution of male psychological mechanisms to attend to women's WHR.

For example, another hypothesis proposes that selection shaped male psychology to attend to women's WHR because it reliably cues *reproductive age*. Consistent with this hypothesis, an inverse relationship between women's WHR and age-linked reproductive capacity has been documented across numerous WEIRD and non-WEIRD populations: female WHR decreases with puberty and the onset of menarche, and then increases with age after peak fertility is reached (see Bovet, 2019, for review). This hypothesis is complicated, however, by the fact that age can be assessed through numerous other cues, ranging from skin and hair quality (see below) to breast development and other secondary sexual characteristics. Such cue redundancy can prevent the evolution of psychological systems to attend to a particular cue—even if that individual cue has the greatest predictive validity (see Iwasa & Pomiankowski, 1994).

However, attending to and integrating redundant cues can reduce inferential errors (Johnstone, 1996). If the benefits of the increase in inferential accuracy outweigh the costs associated with the development and maintenance of neuropsychological systems to attend to and integrate redundant cues, selection can shape mechanisms that attend to multiple cues to the same underlying information (see Johnstone, 1996). Whether this is the case for WHR as a cue to reproductive age remains to be resolved.

In sum, the best evidence currently available suggests that the parity hypothesis is the most theoretically plausible and empirically compelling account for why male psychological systems attend to women's WHR and regulate attractiveness assessments in response to it. Nonetheless, we eagerly await further testing of this and more than a dozen other evolutionary hypotheses about the function of WHR-tracking mechanisms.

ANDROGEN-LINKED FEATURES

Several hypotheses propose that androgen-linked traits in men, such as muscularity, height, and specific facial structures, may convey fitness-relevant information.

One broad hypothesis is the costly signaling hypothesis: that androgen-linked features are costly to develop, and therefore cue phenotypic and possibly genotypic quality. Within this costly signaling perspective, some research has proposed that testosterone has direct immunosuppressive effects and that androgen-linked features cue men's immunocompetence specifically (e.g., see Al-Shawaf et al., 2017; Thornhill & Gangestad, 2006). Other work suggests that these traits are a costly signal but for reasons not directly related to immunocompetence (e.g., see Kokko et al., 2003). For example, greater body size—whether because of greater height, muscle mass, or both—increases energy demands and reduces the capacity to allocate resources to other aspects of somatic upkeep and immune function (Buchanan et al., 2001; Salska et al., 2008).

There is some, albeit limited, evidence suggesting an association between androgen-linked features and individual quality. This includes links to health-related variables such as respiratory disease duration (Thornhill & Gangestad, 2006) and hepatitis B vaccine antibody response (Skrinda et al., 2014), as well as to developmental stability. However, these links may be mediated by factors such as nutrition, lower exposure to pathogens, and greater access to resources during ontogeny (Perkins et al., 2016).

An alternative to the costly signaling hypothesis is that androgen-linked traits are associated with the ability to obtain and defend resources, including

reproductively relevant resources via intrasexual mating competition (Puts, 2010; Puts et al., this volume; see also Caton & Lewis, 2021a, 2021b). Future research is needed to determine which of these is correct, if any. For now, it appears safe to conclude that at least some androgen-linked traits are associated with fitness-relevant outcomes. If this is correct, selection might have shaped psychological mechanisms in women's minds to track these cues and regulate perceptions of attractiveness in response to them.

Numerous studies suggest that women's attractiveness-assessment mechanisms track androgen-linked cues in men. Muscularity (Frederick & Haselton, 2007; Sell et al., 2017; see also Caton & Lewis, 2021b), androgen-linked facial features (DeBruine et al., 2010; Johnston et al., 2001), and height (Salska et al., 2008) all have demonstrated influences on women's perceptions of men's attractiveness. More muscular men also report more lifetime sexual partners, short-term sexual partners, and affairs with mated women (Frederick & Haselton, 2007), and taller men experience greater long-term mating success (see Pawlowski et al., 2000).

Other studies suggest that women perceive faces with *low* levels of androgen-linked features to be more attractive (e.g., Alharbi et al., 2020). Penton-Voak et al. (1999) proposed that variation in women's preferences for male facial masculinity may reflect a trade-off: the direct genetic benefits for offspring may only exceed the costs of lower investment from high-androgen men when women are likely to conceive. However, recent evidence suggests that female preferences for height and muscularity are linear and robust (Sell et al., 2017). These divergent results for (1) facial masculinity and (2) other androgen-linked features, such as muscularity, suggest that these distinct cues may not tap the same fitness-relevant dimensions. A recent meta-analysis corroborates this: all androgen-linked features *except* facial masculinity appear to be associated with greater mating success (Lidborg et al., 2021). Strength and muscularity were the strongest and most consistent predictors of outcomes relevant to mating success, which included indicators of outcompeting other men (i.e., intrasexual selection) as well as female mate choice (i.e., intersexual selection). We eagerly await the publication of this meta-analysis in a peer-refereed journal, as it could offer invaluable insight into (1) androgen-linked features as costly signals, cues to the ability to obtain and defend resources, or indicators of other fitness-relevant information; (2) whether different features, such as facial masculinity and muscularity, cue distinct dimensions of fitness-relevant information, and (3) whether women's information-processing mechanisms respond differently to these distinct cues.

LUMBAR CURVATURE

Women's lumbar spine is unique in the animal kingdom. As the only extant bipedal primates—and because men do not get pregnant—women are the only existing organisms that face the adaptive problem of a forward-shifting center-of-mass during pregnancy. Selection shaped a morphological adaptation to this problem: wedging in the third-to-last lumbar vertebra. This wedging is present in the spines of human females but absent from the spines of human males and both male and female quadrupedal primates (Whitcome et al., 2007), consistent with the fact that only female bipedal primates face the adaptive problem of an anteriorly shifted center-of-mass during pregnancy. Indeed, this wedging *is* present in the fossilized remains of females—but not males—of extinct bipedal hominin lineages (see Whitcome et al., 2007).

This morphological adaptation has critical fitness implications for women, their mates, their developing fetus, and any existing dependent offspring. Without this vertebral wedging, women's ability to shift the gravid center-of-mass would be dramatically impaired, and they could experience as much as an eightfold increase in hip torque during pregnancy (Whitcome et al., 2007). This would have resulted in protracted contraction of women's lower back muscles, resulting in muscular fatigue, increased risk of debilitating back injury, and impaired foraging ability (see Whitcome et al., 2007). Given that women provide a substantial number of calories to the family diet in traditional (e.g., forager) societies, a reduction in a woman's foraging capacity could have subjected her, her mate, their developing fetus, and any existing offspring to malnutrition.

These consequences of women's lumbar vertebral wedging set up selection pressures for the evolution of male psychological mechanisms to attend to cues of vertebral wedging. Women's lumbar (lower back) curvature is a reliable, externally observable cue to this wedging (George et al., 2003). Based on this, we should expect selection to have favored male psychological mechanisms to attend to women's lumbar curvature and regulate mating attraction accordingly. Too little vertebral wedging (hypolordosis) would have been associated with the inability to shift the gravid center-of-mass back over the hips, but *excessive* vertebral wedging (hyperlordosis) also carries fitness costs. Excessive wedging increases shearing forces that can lead to severe injuries such as herniated discs (see Whitcome et al., 2007). Consequently, selection should have favored male psychological mechanisms that produce the highest attractiveness judgments in response to an angle of lumbar curvature that cues the capacity to recenter the gravid center-of-mass over the hips but does not shade into excessive wedging and associated shearing forces on the spine.

Lewis et al. (2015) tested this hypothesis, now known as the *fetal load*

hypothesis (see Lewis et al., 2021). The hypothesis proposes that men will be most attracted to an angle of lumbar curvature that minimizes the net fitness costs of insufficient and excessive vertebral wedging, but it does not specify the value of this angle. Lewis et al. (2015) consulted the medical orthopedic literature to identify the angles of lumbar curvature associated with the fitness threats of hypolordosis and hyperlordosis. They predicted that men would prefer an angle of lumbar curvature maximally distant from these countervailing threats. According to the medical orthopedic literature, that angle is approximately 45.5° (see Fernand & Fox, 1985; Lewis et al., 2015). The researchers tested this proposed male preference by presenting men with images of opposite-sex morphs that systematically varied in their degree of lumbar curvature. Consistent with the fetal load hypothesis, men's perceptions of women's attractiveness peaked at approximately 45.5°—morphs with lumbar curvature values both below and above this value were perceived as less attractive. Subsequent work by Lewis and colleagues demonstrated that this preference cannot be attributed to a preference for greater buttock mass (see Lewis et al., 2015, Study 2); that high heels increase perceptions of women's attractiveness only when donning them shifts women's lumbar curvature closer to the proposed fetal load optimum (Lewis et al., 2017b); and that men track women's angle of lumbar curvature even when presented with female stimuli that are in motion (Lewis et al., 2021).

SKIN

As the natural barrier between the body's internal and external environments, the skin plays an essential role in protection against mechanical, chemical, and ultraviolet damage, as well as infection by microorganisms. Variability in skin quality provides information about numerous fitness-related variables, including the environment to which an individual has been exposed, as well as how the individual has responded to that environment.

Skin texture provides information about both current and long-term nutritional state, with many nutritional deficiencies being associated with skin disorders. Malnutrition causes skin dryness, and vitamin deficiencies—whether the result of malnutrition, malabsorption, or genetic defects—are associated with skin abnormalities, including inflammation, hyperpigmentation, and impaired healing of wounds (see Piccardi & Manissier, 2009, for review).

Irregular skin texture can also cue health issues. Psoriasis, an inflammatory disease linked to immune dysregulation, is characterized by the presence of thick, scaly red plaques (Feng et al., 2009), and, in women, ovary malfunction and overproduction of androgens is linked to skin lesions (Schiavone et al.,

1983). Conversely, smooth skin texture cues the ability to heal without infection (Sugiyama, 2004a).

Because skin quality is linked with age, it may also be a reliable cue to fertility and future reproductive capacity. Damage to the skin accumulates with time; fine lines, wrinkles, and unevenness in skin color increase with age (Farage et al., 2009). Consequently, smooth, homogeneous skin may reliably cue youth and residual reproductive value.

Although future research is needed to determine precisely which fitness-related information is conveyed by distinct skin-based cues, it appears safe to assert that numerous features of the skin communicate important information about several dimensions of mate quality. We should therefore expect selection to have favored attractiveness-assessment mechanisms that track skin quality in potential mates and regulate perceptions of attractiveness in response to it.

Numerous studies support this hypothesis. Skin texture influences perceptions of attractiveness in both men and women (e.g., Fink et al., 2001), and skin smoothness and color homogeneity increase perceptions of women's attractiveness (e.g., Fink et al., 2018). We are unaware of any studies that demonstrate effects in the opposite direction or an absence of these effects; available evidence uniformly suggests that human information-processing mechanisms attend to cues to skin quality and regulate perceptions of attractiveness in response to it.

HAIR

Like skin quality, hair length and quality may reliably cue age, and therefore fertility and future reproductive capacity. With age, hair becomes thinner and dryer (Trüeb, 2009) and is more susceptible to breakage; hair strength is highest at around twenty years of age, after which it declines (Naruse & Fukita, 1971). Research has also found that hair grows fastest around the ages of peak fertility and that hair qualities such as shine, volume, and smoothness are predictive of women's health, youth, and reproductive capacity (see Etcoff, 1999; Hinsz et al., 2001). Consistent with this, women's hair becomes coarser and more brittle following pregnancy and with advanced age (see Symons, 1995).

Hair also conveys information about nutritional status. For example, low levels of keratin, fatty acids, protein, vitamins, and minerals in the diet are all associated with dry, brittle, and dull hair (Haneke & Baran, 2011). Additionally, deficiencies in iron and Vitamin D are linked with reduced hair growth and hair loss (see Amor et al., 2010; Karadağ et al., 2011).

Further research is needed to tease apart distinct hair-based cues and the different fitness-related information they convey, but current evidence suggests

that shiny, strong (i.e., not brittle) hair may provide information about numerous fitness-relevant variables. Consequently, selection should have shaped attractiveness-assessment mechanisms to attend to hair length and quality.

There appear to be only a few empirical studies that have investigated the relationship between these features of hair and perceptions of attractiveness. Longer hair in women is associated with greater attractiveness (see Grammer et al., 2002), an effect that is independent of facial attractiveness (Bereczkei & Mesko, 2006). Hair density and fiber diameter also appear to have independent effects on perceptions of attractiveness (Fink et al., 2016). We await future tests of the relationship between these features of hair and perceptions of attractiveness, as hair appears to reliably cue multiple dimensions of important fitness-relevant information.

TEETH

Dental state cues multiple dimensions of fitness-relevant information. Misaligned teeth are associated with a reduced capacity to break down food in preparation for swallowing and digestion (Helkimo et al., 1978). Discolored teeth can cue metabolic, inherited, and traumatic factors, as well as environmental and dietary issues (Joiner, 2004), including poor nutrition (Bartlett et al., 2011). They also cue aging; textural changes associated with age result in the teeth becoming darker and yellower with time (Odioso et al., 2000). Tooth wear is also associated with age (van't Spijker et al., 2009) as well as with poor nutrition, and tooth loss is linked to nutritional deficiencies (Kim et al., 2007).

Given the links between dental state and these fitness-relevant variables, we should expect selection to have shaped attractiveness-assessment mechanisms to track these tooth-based cues and regulate attractiveness perceptions accordingly.

Evidence supports this hypothesis but is relatively sparse. Aligned teeth are associated with perceptions of the "best smiles" (Koidou et al., 2018) and increased perceptions of attractiveness (Sena et al., 2017). Decay, yellowing, and abnormal spacing of teeth are all associated with decreased attractiveness (see Hendrie & Brewer, 2012). Cosmetic dentistry provides corroborating anecdotal evidence; the industry revolves around creating the impression of straighter and whiter, not more crooked or yellower, teeth (see Sarver, 2004).

In sum, teeth may reliably cue multiple dimensions of fitness-relevant information. However, compared to other cues with less reliably demonstrated links to fitness-related outcomes, there is a relative scarcity of research testing the relationship between perceptions of attractiveness and different aspects of individuals' dentition.

THE EYES: SCLERA AND LIMBAL RING

When asked to describe the different "parts" of the eye, the typical person will identify the pupil, the "colored part" (iris), and the "white part" (sclera). This leaves out (1) *variability* in the color of the sclera and (2) the dark, semi-opaque boundary between the sclera and iris, known as the limbal ring—which also varies both between individuals and within individuals across time.

Sclera. The whiteness of the sclera is a reliable cue to a multitude of fitness-related variables. Because the sclera itself is not pigmented, nonwhite coloration can reveal multiple conditions. Reddened sclera can indicate conjunctivitis, blepharitis, keratitis, iritis, and scleritis, as well as corneal abrasion, the presence of a foreign body, glaucoma, and subconjunctival hemorrhage (Cronau et al., 2010). Yellowing of the sclera may reflect jaundice, which is a cue to hepatic issues or problems with the gallbladder, pancreas, or blood (Roche & Kobos, 2004). Reddening, yellowing, and other deviations from whiteness in the sclera are also associated with senescence (Russell et al., 2014).

Because scleral whiteness is inversely related to these fitness-relevant variables, we should expect selection to have shaped psychological mechanisms to attend to the whiteness of individuals' sclerae and regulate perceptions of attractiveness accordingly. Robust and reproduced empirical evidence from multiple independent laboratories bears out this hypothesis. Individuals with redder, yellower, or otherwise darker sclerae are perceived as less attractive (see Provine et al., 2013).

Limbal ring. The limbal ring is a dark, semiopaque boundary between the sclera and the iris. Available evidence suggests that the limbal ring may be a cue to multiple fitness-related variables. First, it is a potential cue to youth. The deposition of fat and cholesterol on the outer edge of the cornea that occurs with older age results in a lighter limbal ling, and the limbal ring gets lighter and decreases in width with age (see Zheng & Xu, 2008). Second, the limbal ring may cue health status. Among younger individuals, corneal arcus, which results in a lighter limbal ring, may cue excessive cholesterol levels and associated health issues (see Barchiesi et al., 1991; Morris, 1992). Wilson's disease, a genetic disorder in which the liver is unable to properly process and excrete copper, is linked to impaired hepatic, neurological, renal, hematological, and endocrinological function—and it causes copper deposits in the eye that result in a lightening of the limbal ring (Das & Ray, 2006).

If the limbal ring is a reliable cue to these fitness-related outcomes, then we might expect selection to have favored psychological mechanisms to attend to

the prominence of people's limbal rings and regulate perceptions of attractiveness accordingly. Available empirical evidence suggests that this may be the case (see Brown & Sacco, 2018; Peshek et al., 2011). Nonetheless, future research is needed to (1) more precisely identify the fitness-relevant variables cued by the limbal ring, (2) determine the extent to which the limbal ring cues fitness-related information that is nonoverlapping with that indexed by the sclera (e.g., both are hypothesized cues to age), (3) establish whether the limbal ring and sclera have independent effects on perceptions of attractiveness, and (4) more clearly resolve whether the effects of the limbal ring on attractiveness are sex-differentiated (e.g., Brown & Sacco, 2018)—or not (Peshek et al., 2011).

When: Variation in Standards of Attractiveness as Evidence of Context-Sensitive Design

In their paper in *Nature*, Yu and Shepard (1998) suggested that variability in standards of attractiveness across cultures is evidence that "standards of beauty are instead no more than artefacts of culture" (p. 321). This assertion is based on a fundamental misunderstanding of the universal human nature proposed by evolutionary psychologists. This universal human nature refers to species-typical *information-processing systems*, not universal behavior (Tooby & Cosmides, 1990; see also Al-Shawaf et al., 2019; Al-Shawaf & Lewis, 2017; Lewis et al., 2017a). By definition, the output of these information-processing systems is not fixed but rather is contingent on the inputs that the system processes from its environment. These inputs include not just the fitness-relevant cues observed in a potential mate, but also diverse other inputs that range from features of the local ecology to physiological indicators of the perceiver's own current condition (e.g., current immunological status). We know, from abundant psychological and nonpsychological examples in humans and nonhuman animals (and diverse nonanimal taxa, for that matter—from plants to protists), that evolved information-processing systems are designed to produce variable output, contingent on these numerous inputs from the environment (see Lewis et al., 2020). Humans' attractiveness-assessment mechanisms are no exception.

Much more work is needed in order to map the context-sensitivity of the information-processing mechanisms responsible for producing perceptions of attractiveness. Currently, the corpus of literature on such contextual effects is a hodgepodge. Some research has directed attention to a specific contextual variable (e.g., short-term vs. long-term mating). Other research has focused on a specific cue in conjunction with contextual variables that shift the fitness value of that cue. Some contextual effects have been discovered based on rigorous

theorizing and a priori hypotheses. In other cases, contextual effects have first been observed and then explained. And when this has occurred, some of these post hoc explanations have been followed up with the generation of new, testable hypotheses as part of the complete process of observation-driven science. In other instances, these explanations have been left as little more than speculations.

A broader, more systematic approach is needed that follows three key steps. Researchers should (1) identify specific contextual variables that ancestrally shifted the fitness value of the cues discussed above (as well as as-yet-unidentified fitness-relevant cues), (2) generate a priori hypotheses about how attractiveness-assessment mechanisms should shift their output in response to these contexts, and (3) test for this hypothesized variation.

By and large, the literature has not been characterized by such a systematic approach. Nonetheless, researchers have made some important strides toward documenting the evolved context-sensitivity of humans' attractiveness-assessment mechanisms. Here, we provide a brief sampling of evolutionarily patterned contextual variation in perceptions of attractiveness.

ANDROGEN-LINKED FEATURES

Androgen-linked features in men have been hypothesized to cue immunocompetence and the production of robust offspring—but also low levels of paternal investment. The trade-off between these hypothesized genetic benefits to offspring and the costs of low levels of paternal investment shifts across environments; the benefits of producing robust offspring are greater in environments characterized by environmental stressors that threaten survival. Consequently, we should expect selection to have shaped women's attractiveness-assessment mechanisms to place greater value on androgen-linked cues in men in environments characterized by higher mortality rates and communicable disease. DeBruine et al. (2010) tested this hypothesis by investigating variability in women's preferences for male facial masculinity across thirty countries. Precisely as predicted, women's preference for androgen-linked cues in men was greater in countries characterized by high levels of environmental stressors that could threaten survival.

SYMMETRY

Symmetry has been hypothesized to cue the ability to withstand environmental stressors, which can lead to perturbations during development. If so, then (1) individuals should exhibit higher mean levels of asymmetry in environments characterized by higher levels of environmental stressors, and (2)

the fitness value of symmetry should be higher in such environments because it is a more reliable cue of individual quality. Consistent with the first proposition, Gray and Marlowe (2002) demonstrated that mean levels of asymmetry among foraging populations are higher than those observed in WEIRD populations. Little et al. (2007) investigated the second hypothesis by testing preferences for symmetry across two cultures: the United Kingdom and the foraging society of the Hadza of Tanzania, which, relative to the UK, has significantly higher mortality rates throughout the lifespan. Precisely as hypothesized, the Hadza exhibited a stronger preference for symmetry than did individuals from the UK.

WAIST-TO-HIP RATIO

For women's WHR, we describe research that has documented several contextual effects, including one that provides unique insight into the developmentally open design that evolved psychological mechanisms may have. Several studies have documented a preference among people from foraging societies for a female WHR that is higher than that preferred in industrialized nations (e.g., see Marlowe & Wetsman, 2001; Wetsman & Marlowe, 1999; Yu & Shepard, 1998). However, Sugiyama (2004b, 2015) noted that the stimuli employed in these studies appeared to conflate body fat and WHR, and his closer examination revealed two distinct, systematic effects of context. First, individuals from foraging societies appear to prefer mates with higher levels of body fat. This aligns with the notion that body fat stores have greater fitness value in conditions characterized by the threat of food shortages, and that selection therefore shaped human attractiveness-assessment mechanisms to place greater value on body fat stores under food-scarce conditions (e.g., Swami & Tovée, 2006; see also Sugiyama, 2004b). Even after taking these variable preferences for body fat into consideration, people from foraging populations *still* appeared to exhibit a preference for a higher WHR than people from WEIRD societies. However, when WHR values were standardized relative to local population distributions, the same finding emerged across WEIRD and non-WEIRD populations: a preference for *locally* low WHR (see Sugiyama, 2015, for discussion). This suggests that attractive-assessment mechanisms are somewhat *developmentally open* (see Hagen & Hammerstein, 2005): rather than producing an invariant preference for a fixed value of a cue, attractiveness-assessment mechanisms may instead be designed to learn about variability in that cue in the local socioecology and then produce preferences for values of that cue (in this case, low values) relative to the local distribution (Sugiyama, 2004b; 2015; see also Tovée et al., 2006). Such developmentally open design features of evolved psychological mechanisms (1) illustrate that learning and evolution are

deeply interconnected and complementary—not competing—explanations (Al-Shawaf et al., 2019) and (2) represent an exciting avenue for future research.

Further Context Effects: Other Cues, Contexts, and Design Features

This brief sampling illustrates that human information-processing mechanisms respond to specific cues differently in different contexts as a function of the distinct adaptive problems posed by those contexts. This systematic, patterned variability in human standards of attractiveness across contexts is often predictable a priori on the basis of evolutionary reasoning and does not conflict with the notion of evolved, species-typical design (e.g., Al-Shawaf & Lewis, 2017).

In the future, we hope to see more systematic and theoretically driven investigations into contextual influences on perceptions of attractiveness. This should include investigating (1) context effects for all hypothesized fitness-relevant cues, (2) a wider range of contextual variables that shift the fitness values of these cues, and (3) a more diverse set of context-sensitive design features.

Investigating Context Effects for All Hypothesized Fitness-Relevant Cues

Contextual effects have not been systematically investigated for all hypothesized cues. In some cases, this may be because the cue (e.g., lumbar curvature) was only recently discovered, but in other cases (e.g., women's WHR), it is unclear why there have been so few investigations of context effects. Even a brief consideration of contextual shifts in the fitness value of women's WHR can yield new, testable predictions. As discussed above, a leading hypothesis for why the male mind tracks women's WHR is the parity hypothesis (see Lassek & Gaulin, 2006, 2019). As a woman's parity increases, her future reproductive potential decreases. To the extent that future reproductive potential is more important in long-term mating than in short-term contexts, we might expect attractiveness-assessment mechanisms to place greater value on women's WHR in long-term than short-term contexts—if the parity hypothesis is correct. An alternative hypothesis is that the male mind tracks WHR as a cue to women's probability of conception. If a woman's immediate probability of conception is more important in short-term than long-term mating contexts, we also might expect an effect of mating context—but in the opposite direction. This suggests that contextual influences not only await discovery but also may be indispensable for adjudicating between competing evolutionary hypotheses.

Investigating a Wider Range of Contextual Variables

Researchers should also explore a more diverse set of contextual variables, as there are a number of such variables that shift the fitness value of a given cue. Significant attention has been directed to mating context-based (i.e., short-term vs. long-term) shifts, and such work has yielded empirical fruit. The influences of some other key variables have also been investigated, including resource scarcity and food deprivation; pathogen prevalence, mortality rates, life expectancy, and other indicators of environmental stressors and ecological harshness; and operational sex-ratio and other proxies for mating competition. We encourage researchers to continue to explore the influences of these contextual variables, but across the gamut of fitness-relevant cues rather than on just one cue at a time (e.g., DeBruine et al., 2010; Sugiyama, 2004b). We also encourage researchers to think broadly about ecological, social, and conditional (i.e., dependent on the perceiver's phenotype) variables that may influence the fitness value of a given cue (see Jennions & Petrie, 1997). For example, despite the productivity of research on shifts in the perception of attractiveness as a function of shifts in mating *context*, there is a comparative paucity of research investigating how individual differences in mating *strategy* may predict variability in perceptions of attractiveness. This is surprising, given that the logic for strategy-based shifts is virtually identical to that for context-based shifts. How individual differences in mating strategy interact with shifts in mating context (e.g., when long-term-oriented individuals are presented short-term mating opportunities) is even less explored.

Investigating a More Diverse Set of Context-Sensitive Design Features

Finally, the existing body of work on context effects has focused largely on just one type of context-sensitive design feature: shifts in the preferred *level* of a cue. For example, DeBruine et al. (2010) demonstrated that women from countries characterized by higher levels of threat to survival prefer greater *levels* of facial masculinity in men. This is sometimes referred to in the literature as a "stronger" preference for masculinity, but such usage conflates two distinct features of attractiveness-assessment mechanisms. Attractiveness-assessment mechanisms should adjust both (1) the preferred *level* of a trait and (2) the *strength* of that preference (i.e., how much value or weight is placed on that trait) across contexts. These are two different types of design feature. This distinction is important because, in some cases, the preferred level of a cue—but not necessarily the strength of the preference—should shift across contexts. In other cases, the opposite should be true. For example, if a higher WHR has greater fitness value in environments characterized by unpredictable food resources, then we should expect the preferred *level* of WHR to shift as a function of food

reliability, but we might not necessarily expect the value placed on WHR in overall attractiveness assessments to change. Conversely, in short-term contexts, mating with an individual who exhibits cues to immediate fertility may be a more pressing adaptive problem than it is in long-term contexts. Consequently, attractiveness-assessment mechanisms might place greater *value* on cues to fertility—but not necessarily prefer a different *level* of fertility cues—in short-term than long-term contexts.

More broadly, investigations that distinguish between the preferred *level* of a cue and the *strength* of that preference are needed. Toward this goal, researchers could profitably employ a more diverse set of tools for measuring preferences. Attractiveness ratings, as well as more advanced measures like slider scales where the participant can manipulate the cue to their preferred level, may not readily capture information about the *strength* of that preference. Other paradigms, such as budget allocation methods and forced trade-offs (e.g., Li et al., 2002; see also Lewis et al., 2011), on the other hand, may be better suited to answer questions about the strength of preference for a particular cue. Moreover, such paradigms will enable researchers to investigate not only the trade-offs associated with different levels of a single cue, but also trade-offs between multiple cues across contexts. For example, attractiveness-assessment mechanisms may trade off cues to future reproductive potential for cues to immediate fertility in short-term mating contexts but may do the opposite in long-term contexts. Attending to these kinds of trade-offs would be both theoretically and empirically valuable.

Other Cues: Different Perceptual Modalities and Different Relationship Types

In this chapter, we have focused on the perception of physical attractiveness in response to cues that are *morphological*, *visual*, and of fitness relevance to human *mating* relationships. Covering the entire landscape of cues relevant to interpersonal attraction is beyond the scope of a single chapter, but we wish to briefly discuss what a comprehensive discussion of human interpersonal attraction must include.

First, the mind evolved to attend not just to *visual* cues, but also to fitness-relevant cues detectable via other perceptual modalities, including auditory (e.g., Puts et al., 2011), olfactory (e.g., Jacob et al., 2002), tactile, and gustatory cues (see Caton et al., in press, for a discussion of human intersexual courtship via these distinct perceptual modalities). Abundant evidence also indicates that the

mind evolved to attend to cues that are not directly produced or emitted by the target. For example, there is robust evidence that women's psychological mechanisms track cues to men's social and economic *status* and integrate this information with other aspects of mate value to regulate mating attraction (e.g., see Buss, 1989; Buss et al., 2020; Buss & Schmitt, 1993). In short, visual cues represent just one class of perceptual cues that influence the perception of an individual's physical attractiveness—and the perception of an individual's physical attractiveness is only one facet of the perception of an individual's overall mate value.

Moreover, mating attraction is only one portion of the broader landscape of interpersonal attraction in human relationships, of which there are diverse types —from short-term sexual liaisons to long-term committed partnerships, from temporary coalitional alliances to lifelong friendships. In cases where the fitness value of a cue varies across relationship types, we should expect human psychology to respond to that cue differently across distinct relationship types. We encourage the reader interested in interpersonal attraction in nonmating relationships to consult Sugiyama (2015) for a discussion of the broader concept of individuals' "social value" for nonmating relationships (see also Petersen et al., 2012).

Moving Forward: Greater Specification of Hypotheses and Design Features

An evolutionary approach to attractiveness is both indispensable and in need of several major improvements. Without this approach, many findings in attractiveness research would have seemed arbitrary and remained unexplained, and many *previously unknown* influences on attractiveness might have remained undiscovered. Despite these key contributions, we call for several key improvements in evolutionary research on attractiveness. These suggested improvements all derive from the overarching suggestion that hypotheses should be anchored more deeply in the *information-processing mechanisms* responsible for producing perceptions of attractiveness. A closer focus on these mechanisms and their design features will lead to a more precise specification of these hypotheses and a clearer picture of the predictions they generate. This will render the hypotheses more readily falsifiable, facilitate pitting them against competing evolutionary accounts, and, ultimately, lead to new discoveries about what humans find attractive and why.

When a hypothesis is underspecified—when it fails to identify, in advance,

the expected design features of the hypothesized mechanism—it becomes difficult to test that hypothesis, let alone pit it against competing alternatives, including alternative evolutionary hypotheses. This underspecification of hypotheses can manifest itself at different stages of hypothesis generation. It can first arise when a researcher fails to specify the fitness-relevant variable supposedly linked to the cue of interest in the first place (Bovet, 2019). This is a critical first stage of hypothesis generation. If a hypothesis fails to do this, then it becomes difficult or impossible to generate predictions about how the perception of attractiveness in response to that cue should vary as a function of specific contextual variables. Bovet (2019) highlighted that the evolutionary literature on WHR is rife with such hypotheses, which are "vague theoretical explanation[s]" that present a nebulous argument about a particular cue being predictive of an individual's "mate value" based on some invocation of "health," "fertility," or some combination thereof (p. 3). Even if we temporarily accept the broad constructs of "health" and "fertility" as sufficiently specific, these are *different* fitness-relevant variables. Immediate *fertility* would appear to have greater relevance in short-term mating contexts than in long-term contexts. By contrast, a potential mate's *health* would certainly seem to be important for long-term mating decisions. The broader point is this: it is necessary for researchers to be explicit about the fitness-relevant information hypothesized to be indicated by the cue in order to generate predictions about the design of the information-processing mechanism that attends to that cue.

Clearly specifying the fitness-relevant information indicated by the cue will enable researchers to generate predictions about the design features of the mechanism, thereby rendering the hypothesis more readily testable. In particular, generating predictions about how the mechanism should respond to that cue across different contexts will enable more specific tests of the hypothesis *and* enhance researchers' ability to pit the hypothesis against alternative evolutionary accounts.

The WHR literature again illustrates this point well. Bovet's (2019) systematic review revealed that at least seventeen evolutionary explanations have been proposed for why men's attractiveness-assessment mechanisms attend to women's WHR. For each of these hypotheses, the specific fitness-relevant variable hypothesized to be cued by WHR should provide insight into the information-processing architecture of the proposed mechanism. For example, one hypothesis proposes that the male mind tracks WHR because lower levels of WHR are associated with greater openness to short-term mating. If this hypothesis is correct, we should expect men's attractiveness-assessment mechanisms to place greater value on low WHR in short-term than long-term

contexts. By contrast, a different hypothesis proposes that the male mind tracks WHR because it is a cue to "maternal behavior" (Bovet, 2019, p. 12). If this hypothesis is correct, we should expect precisely the opposite context effect: men's attractiveness assessment mechanisms should place greater value on low female WHR in long-term than short-term mating contexts.

Together, these two contrasting hypotheses illustrate several points. First, they demonstrate the importance of being specific about the fitness-relevant information indicated by the cue; this specificity is essential for researchers to generate a priori predictions about the design features of the hypothesized information-processing mechanisms, including their sensitivity to contextual variables. Second, research needs to test for evidence of these design features. By testing for evidence of the *different* information-processing design features expected under competing hypotheses, researchers will be able to empirically adjudicate between alternative evolutionary explanations. Third, the existing shortcomings of the evolutionary literature on attractiveness truly do represent valuable future opportunities. Rather than simply discarding the loosely specified hypotheses that have been advanced, researchers can and should return to them in order to specify and test for the information-processing design features that they propose.

We hope that this approach—clearly articulating the fitness-relevant information hypothesized to be linked to the cue and generating specific predictions about how attractiveness-assessment mechanisms should respond to that cue across different contexts—is useful for refining existing hypotheses as well as for generating new hypotheses about humans' psychology of attractiveness. Ultimately, we hope that this leads to exciting new discoveries about what humans find attractive, when, and why.

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CHAPTER
8

Incest Avoidance Adaptations: Evolved function and proximate mechanisms

Debra Lieberman and Carlton Patrick

Abstract

Humans, like many social species, interact with genetic relatives throughout periods of sexual maturity increasing the chance that, barring systems motivating avoidance, close genetic relatives could select one another as sexual partners. However, although suitable in several respects, close genetic relatives represent poor sexual partners due to selection pressures posed by short-generation pathogens and lethal recessive mutations. For this reason, it is likely natural selection crafted information-processing circuitry—mental software—that enabled inferential systems to estimate the probability another individual was a close genetic relative and to trade off this information against other factors influencing fitness to adaptively identify suitable sexual partners. In this chapter we discuss incest avoidance adaptations and provide a model of how human mate choice might operate.

Key Words: Mating, kinship, incest avoidance, inbreeding, sexual psychology

Why don’t humans select close genetic relatives as sexual partners? This might seem an odd question, but to biologists, whenever you see members of a species engage in what seems to be strange and costly behavior, it raises questions of selection and function. In the case of inbreeding avoidance, consider the seemingly strange trend: humans go out of their way to avoid mating with individuals with whom they are most likely to share values, interests, preferences, religion, culture, friends, and habitat—and instead, gamble

on someone with whom they share far less history, and, all else equal, is far more likely to exploit them. Why bother with this nonsense when putatively healthy, attractive, and caring family members are right down the hall? In this chapter, we "make the natural seem strange" to quote William James (1890), and address why inbreeding avoidance adaptations evolved and how they achieve their function.

Inbreeding, Pathogens, and Mutations

The reason we typically don't covet family members relates to the reason why sexual reproduction evolved. Sexual reproduction is an adaptation that evolved in response to the substantial selection pressures posed by pathogens—short-generation micro-organisms that exploit hosts in an effort to promote their own reproductive success (Bremermann, 1980; Tooby, 1982; Williams, 1975). There is a vast difference between the rates of replication of pathogens as compared to their hosts resulting in a pathogen–host dynamic with asymmetrical rates of evolution (Hamilton, 1980; Tooby, 1982). Indeed, during one host generation, infectious pathogens cycle through numerous iterations of selection and reproduction, learning how to evade components of internal defense systems and how to capture host resources in their own struggle to survive and replicate. This relative time lag in host reproduction presents pathogens with a more or less stable environment to which they can adapt, ultimately increasing their ability to exploit their hosts.

Hosts have evolved a set of defenses to stem the tide of invasive microorganisms and one effective defense is sex (Hamilton, 1980; Levin, 1975; Tooby, 1982). The benefits of sex are more easily seen when one considers first asexual reproduction. Asexual reproduction maintains a more or less constant genetic environment down the generations; offspring resemble parents in almost every respect. Under these conditions, bacteria, viruses, and other microorganisms would have an advantage when colonizing and adapting to offspring. In general, all the generations that pathogens spent adapting to the specific characteristics of an asexually reproducing host would still be useful when the pathogens got transferred to new, identical offspring. The pathogens thus stay ahead in the pathogen–host arms race, increasing the risk of pathogen exploitation. This is one reason why many cloned animals suffer such high rates of mortality (e.g., Ogonuki et al., 2002)—biochemical uniformity favors pathogen evolution.

Sexual reproduction, as compared to the clonal process of asexual reproduction, generates *new* combinations of genes. With sex, pathogens that

might have been well adapted to a particular DNA sequence or its protein product are no longer as well adapted after genomes recombine and produce rare/novel—yet still functional—sequences (Ridley, 1993). We note that an important distinction needs to be made between selection for novel genotypes and selection for rare genotypes, of which novel forms will be a subcategory (see Jaenike, 1978). Different theories of the evolution of sex turn on this distinction (e.g., evolvability vs. moving target theories).

Regardless of whether genotypes are novel or merely rare, sexual reproduction increases the diversity of the internal biochemistry of hosts and pushes pathogens back to square one in their progress toward host domination (Tooby, 1982). Importantly, the advantages of sex are obtained only if individuals recombine genomes with others who *do not share the same genes*. Sex with a clone is no different than asexual reproduction in that it maintains a similar environment to which pathogens can learn to adapt and exploit. And this is why inbreeding generally reduces the reproductive success of an organism and produced systems to decrease its occurrence.

Genetic relatives, by virtue of sharing a common ancestor, have a greater chance of sharing the same genes and, by extension, a similar internal biochemistry. Mating with a genetic relative increases the risk of generating offspring who are more "clone-like" and who will thus suffer from an increased risk of pathogen infection (e.g., Bittles & Black, 2010; Rudan et al., 2010). The closer the relative, the greater the overlap in shared genes and the greater the risk of producing a child vulnerable to disease. The pathogen-induced decrease in the reproductive success of individuals who happen to select more genetically similar mates is one of the main reasons why evolution favored (in humans and in many other species) neural software that causes inbreeding avoidance—the avoidance of close genetic relatives as sexual partners.

Another reason why inbreeding-avoidance systems evolved is because of the existence of harmful genetic mutations (Bittles & Neel, 1994; Charlesworth & Willis, 2009). Humans are a diploid species. We inherit one copy of genes from our mother and one copy from our father. This inheritance system has built-in redundancy: when the gene inherited from one parent is damaged, the gene inherited from the other parent can typically fulfill the required function. We all have damaged genes, which can range in their effects from deadly to slight. Estimates vary, but geneticists have suggested that each individual possesses between 0.29–1.4 recessive genes that, if present in a double dose (because mom and dad both donated the same broken gene), would be fatal (Bittles & Neel, 1994; Gao et al., 2015). We are not dead ten times over because when we inherit one of these mutations, its effects are masked by the functioning allele inherited

from the other parent. Redundancy works. But this redundancy is severely compromised when parents are closely related.

The decrement in fitness of offspring should correspond with the genetic similarity of parents, with the most severe consequences resulting from unions between parents and offspring and between siblings, first-degree relatives who have a 0.5 probability (on average) of sharing a gene identical by virtue of descent (i.e., over and above the random probability of sharing a given with another human). Next consequential would be unions between half siblings, aunts and nephews, and uncles and nieces, relatives who have a 0.25 probability (on average) of sharing a gene identical by virtue of common descent. The negative consequences trail off rapidly as one moves further out on the family tree, as first cousins have a 0.125 probability of sharing genes by virtue of common descent.

There is a large body of evidence showing that inbred children experience a wide range of physical disabilities, cognitive deficits, and health problems (e.g., Bittles et al., 1991; Zlotogora & Shalev, 2010) and they reveal that offspring born from closer relatives experience greater health problems. In one study conducted on Czech women, children sired by the mother's father or brother were six times more likely to suffer severe birth defects or early mortality than children born of the same women sired by an unrelated man (Seemanova, 1971). "Kissing cousins" are relatively less affected but certainly not exempt from these risks: the rate of infant and early childhood mortality for children of first cousins is ~3.5 percent greater than that for children of unrelated parents (Bittles & Black, 2010). The same trend holds for nonhuman species too (e.g., Liberg et al., 2005). By and large, where it has been studied, be it in plants or animals, inbreeding reduces the health and survivability of offspring.

Mating with close genetic relatives, then, increases the risks of transmitting harmful genetic mutations to offspring and creates in offspring internal biochemical environments more hospitable to invading microorganisms. Given these strong selection pressures, one should expect to see systems for identifying close genetic relatives and programs that use this information to motivate sexual avoidance.

The Architecture of Human Kin Detection and Inbreeding Avoidance

A system tasked with avoiding close genetic relatives as sexual partners requires two main components. The first component is a kin detection system—

the ability to determine which individuals, of all the individuals in the current social environment, have a high probability of being a close genetic relative. The second component is a sexual motivation system that takes the probability a given individual is related as input and slams on the brakes whenever that probability gets too high. We consider each component in turn.

Detecting Kin

Relatedness must be inferred, and is done so for many species via the perception of specific cues that tightly correlated with the likelihood of close relatedness (Hepper, 1991; Holmes & Sherman, 1983). Such cues, once detected, could then be taken as input by an intermediate system that computes, *for each individual* in the social environment, an estimate of relatedness (Cosmides & Tooby, 2013; Lieberman et al., 2007). The absence of any kinship cues for a given individual leads to a low, baseline estimate of relatedness. The presence of kinship cues ratchets this estimate upward. The effect that each cue has on the magnitude of the computed relatedness estimate has been set by selection based on the manner in which each cue statistically predicted genetic relatedness over many thousands of generations. That is, the links between kinship cues and the probability of relatedness were "learned" across generations and codified in our neural programming. Once formed, the *estimate of genetic relatedness* is an internal psychological variable that can be taken as input by systems guiding kin-directed behaviors including both sexual avoidance and altruism (Cosmides & Tooby, 2013; Tooby et al., 2008).

But what cues do we use? There are a number of constraints that confine the set of cues selection might have favored to engineer kin detection systems. For instance, barring recent medical technology, we are not able to directly compare genomes to assess kinship. However, other possible kinship cues exist. One possibility includes the use of more evolutionarily novel cultural information such as linguistic kin terms. But these are unlikely to be the primary cues used to detect kin because kin terms can blur genetic boundaries. For instance, the term "aunt" or "auntie" in English-speaking cultures can refer to a parent's sister, a blood relative, and a parent's brother's wife, a nonblood relative. Likewise, kin terms can be used manipulatively as they are in sororities and fraternities and in many political and religious institutions (e.g., band of brothers and Father). Yet despite the application of kin terms, individuals tend to know who their real siblings and parents are (e.g., Chagnon, 1992).

Another problem with linguistically conveyed information is that perceptions of kinship are perspective dependent. For instance, inclusive fitness theory posits

that an individual should favor a full biological sister, who has a 0.5 chance of sharing a particular gene by virtue of sharing the same parents, over a maternal half-sister, who has only a 0.25 chance (the degree of relatedness, *r*, of 0.5 is twice is great as an *r* of 0.25). But the individual's mother sees the world differently, as she is related to both her children equally, $r = 0.5$. She will be motivated to have you "help your sister," without linguistically marking whether that sister is full or half, a factor that only affects *your* decisions, not hers. Given the perspective dependency of kinship, it is unlikely natural selection would have (or even could have) crafted systems to teach another person's relatedness to others, thus rendering language an imprecise mechanism for learning about kinship.

Last, there is good reason to suspect that alternative kin-detection mechanisms were in place long before language evolved. Indeed, many social species, including lions, voles, birds, bees, squirrels, elephants, wolves, and chimpanzees, treat close genetic relatives differently than more distantly related or unrelated individuals (e.g., Hepper, 1991). Specifically, they tend to act more altruistically toward close genetic relatives and to avoid their close genetic relatives as sexual partners. The existence of these behaviors implies that many species possess, somewhere in their psychology, systems for identifying relatives. But none of these species possess a verbal language, and so they cannot rely on it to learn or communicate "this is your sister, so be nice and don't have sex with her." It is unlikely that these phylogenetically prior kin-detection mechanisms that functioned in the absence of linguistic information were overwritten by more variable and potentially less reliable cultural information.

Rather, it is likely we rely on ecologically valid cues that correlated with genetic relatedness in human ancestral environments (Bressan & Kramer, 2015; Park et al., 2008). Importantly, the cues mediating kin detection might differ depending on the type of kin in question. To the extent that different cues signaled an individual was a specific type of close genetic relative (e.g., mother, father, offspring, or sibling), different detection mechanisms are likely to exist. Additionally, males and females might use distinct cues to identify the same type of kin. For example, because men can never be fully certain of their relatedness to offspring, the cues signaling that an infant is indeed one's own are likely to differ for men and women. We walk through the different relationships within the nuclear family.

MOTHERS AND OFFSPRING

Of all the bonds in nature, none is more certain than the relatedness of mother

and offspring. In humans, because fertilization occurs internally, women have an unmistakable cue for identifying their young: birth. Long before the advent of modern medicine, a woman could always be 100 percent certain that the baby coming out of her body was indeed her own. Prolonged care (including breastfeeding) would have allowed mothers to imprint on features of the baby, enabling continued recognition. For the baby in question, a good bet for identifying "mom" or "primary attachment figure" would have been to simply determine who fed you. Ancestrally, babies nursed for two to four years, and the primary person doing the breastfeeding was mom. Although humans engaged in patterns of alloparenting (Hrdy, 2011), the individual most motivated to care for young when fussy, tired, hungry, or ill would have been the female most highly related to the offspring—mom. Circuitry in the baby's head that caused him or her to remember the olfactory, visual, or aural features associated with the feeding machine would have helped to detect which woman, of the group of surrounding women, was most likely mom and thus willing to extend care. Much of the literature in developmental psychology talks about attachment. Kin-detection systems that sift for cues used to infer relatedness are likely a good part of this larger attachment process.

FATHERS AND OFFSPRING

In stark contrast to women, men cannot be 100 percent certain who their child is. The question each man has to answer is: What is the probability that the child coming out of a particular woman is mine? The field is cut substantially by first determining which women the man has had sex with: no sex, no baby. After narrowing the field down to women with whom a man has lain, the questions get more specific: *When* did I have sex with her—many years ago or a few months ago? A pregnant woman with whom a man slept once five years ago could not be carrying his child today, but a woman with whom he slept five months ago could be. Somewhere in the human male mind is, by hypothesis, a timer that indicates the probability of paternity, much as what likely occurs (again, by hypothesis) in males of other species who assess the probability of relatedness of young.

Although not directly applicable to humans, studies of male langurs provide evidence for how such a mechanism might manifest. In langurs, there is one alpha male that controls access to a group of females. When a reigning alpha male is replaced by a new male, the new alpha typically begins to kill all of the nursing young and newborns (e.g., Hanuman langurs; Borries, 1997). This causes the females to begin ovulating again (ovulation is inhibited by the hormones that ramp up milk production). The new alpha will continue to try to

kill newborns up until the time that he could have sired the child. Somehow langur males "know" the timing of their species' reproductive cycle. It is thus not farfetched to hypothesize that in humans, men do too.

In addition to having a tacit understanding of timing, men also need to assess whether the woman in question has had sex with other men and whether this has occurred in the relevant time period. Sexual fidelity is critical to men's ability to infer their relatedness to offspring (Alexandre et al., 2011; Apicella & Marlowe, 2004), and not surprisingly, men around the world tend to hold this trait dear (Buss, 1989). But sexual fidelity is only half the story. Even if a man believed his mate to be 100 percent sexually faithful, would this mean that *any* child she held or fed was his? No. Under ancestral conditions women frequently collaborated in child care, often passing infants around for extended periods of being held by other women (Hrdy, 2011). Thus, basing paternity on which baby one's mate held, independent of other information, would have led to many false positives.

Instead, what is needed beyond assessments of fidelity is the repeated and extended observation of one's mate caring for—breastfeeding—the infant, a "fidelity-feeding" combination of paternity cues (Billingsley et al., 2018). This would allow the man to know that *this particular child* is mine (not the one she carried around for just an hour yesterday). So the logic for paternity assessment in a male's mind might pose the following queries: (1) Did I have sex with this woman? (2) How many times did I have sex with her and during which time window? (3) Is this woman pregnant? (4) What is the likelihood this woman has had sex with other men during the relevant time period? (5) Did I observe her pregnant, feeding, and caring for the infant that resulted approximately ten months after sex with her?

What about the other direction—offspring detection of fathers? Notably, very little research has attempted to pinpoint how children identify their father. But while it's an open question, we can make some educated guesses based on the information available when these systems were formed. For example, humans often had reliable cues to motherness, which included breastfeeding and intensive care. Since males—both human and other mammalian species—do not breastfeed, much of infant caregiving fell on the shoulders of females. What are the cues that would have enabled a child to infer which man, out of the community of men, was likely "dad"? One possibility is that children merely rely on the paternity assessment of men. To the extent that a man is certain that a child is his own, he will likely be motivated to help care for the child (e.g., see Williams & Finkelhor, 1995, who report a link between caretaking and parental feelings in a study on incestuous vs. nonincestuous fathers). All the child would

have to do, then, is to register which man provided the largest investment (in other words, who's doting on me the most? Who's bringing me meat home from the hunt?). Another possibility is that children rely on mom to figure out "fatherness." The man in a relationship with mom starting from when the child was born has a better chance of being dad than a stranger encountered from the next village when the child is ten. Identifying the man in close physical association with mom, sleeping in the same bed as mom, arguing with mom, and caring for mom has a better-than-zero shot at being dad (i.e., most of the time).

SIBLINGS

The ancestral social environment of humans was such that a likely reliable cue to siblingship would have been seeing one's own mother caring for (e.g., breastfeeding) a newborn (Lieberman et al., 2007). Indeed, the intense mother–child association that typically occurs surrounding the natal period and continues throughout the first few years of life would have served as a stable anchor point for others to infer relatedness. Thus, if an individual observed an infant receiving care from the individual's own mother (at least the female categorized as one's own mother), then it was highly probable that that infant was the individual's sibling. Further, exposure to this cue would have signaled genetic relatedness regardless of coresidence (or association) duration. That is, regardless of whether one was five, ten, or fifteen years old, maternal-infant directed care would have cued probable genetic relatedness (Lieberman et al., 2007). However, as potent a cue as mother–infant association might be, it is available only to older siblings already present in the social environment; the arrow of time forbids a younger sibling from having seen his or her older sibling born and cared for as an infant. For younger siblings, then, what cue or cues might evolution have used to identify probable older siblings?

One solution is to track the flow of parental effort. Any child regularly receiving care from one's own mother and father had a higher probability of being kin than children receiving care from other individuals. Moreover, the longer the care, the more likely the individual would have been a sibling. This cue, operationalized as childhood coresidence duration, was first proposed by Edward Westermarck, a Finnish social scientist who noted that children reared in close physical proximity during childhood tend to develop a sexual aversion toward one another later in adulthood (Westermarck, 1921). This idea, known as the Westermarck hypothesis has received support from various anthropological and psychological investigations (see review in Lieberman et al., 2003). Perhaps most notable are the cases of the Israeli kibbutzim and Taiwanese minor marriages, two natural experiments inadvertently created by cultural institutions

in which unrelated children were reared in close physical proximity throughout childhood. As the Westermarck hypothesis predicts, children reared together throughout childhood rarely marry one another (Israeli kibbutzim: Shepher, 1983), and if forced to marry suffer decreased rates of fertility and increased rates of divorce and extramarital affairs (Taiwanese minor marriages: Wolf, 1995; see also Lieberman, 2009). Together, these studies point to early coresidence as one cue our mind uses to assess relatedness and to dampen sexual desires. However, they raise many questions. For example, does coresidence duration predict sexual aversions differently for the younger and older sibling in a sib-pair? As suggested above, older siblings might rely on a different cue to identify probable younger siblings, one that operates independent of coresidence duration. Also, do the same kinship cues that regulate inbreeding avoidance also regulate kin-directed altruism, the other suite of behaviors relying on assessments of relatedness? These and other questions have been and continue to be addressed in the psychological sciences (e.g., Bressan & Kramer, 2015; Hansen et al., 2020; Sznycer et al., 2016).

It is not ethical to subject humans to the life-altering experiments used by evolutionary biologists to study kin recognition in nonhuman animals. For this reason, scientists have either had to look for natural experiments, such as those mentioned above, or take advantage of the natural variation that exists in families composed of actual genetic relatives. To investigate whether a proposed cue serves as a signal of relatedness, it is possible to match individual variation in exposure to the specific cue (e.g., coresidence duration and mother-infant association) to behaviors and reactions relating to sexual behaviors with family members. Converging lines of evidence indicating that we use a particular cue to categorize individuals according to genetic relatedness can be found through investigations of altruism. If the same kin-detection mechanism serves to regulate both sexual avoidance and altruism, then a cue to kinship should show parallel effects across these two distinct motivational systems.

Using this logic, a team of researchers set out to investigate whether our mind evolved to use coresidence duration and maternal-infant association as separate cues for detecting older siblings and younger siblings, respectively. Using surveys to collect information, Lieberman et al. (2007) found that individuals not exposed to their mother caring for their sibling as a newborn (as it is typically for the younger sibling in a sib-pair), their duration of coresidence with an opposite-sex sibling predicted aversions to sibling incest, as measured by disgust at imagining sex with one’s own sibling and moral sentiments relating to third-party sibling incest. By contrast, for individuals exposed to their mother caring for their sibling as an infant (the older siblings in a sib-pair), coresidence

duration with an opposite sex sibling *did not* predict aversion to incest. When measures of altruistic attitudes and behavior were analyzed, the same pattern emerged (Sznycer et al., 2016). That is, coresidence duration with a sibling predicted altruism more strongly for individuals without access to the more potent cue of seeing their mother caring for their sibling as a newborn. These data provide compelling evidence that the mind uses two different cues for identifying older versus younger siblings and for regulating sexual aversions and altruistic motivations.

Upon inspecting the levels of aversions and altruistic inclinations reported, Lieberman et al. (2007) found that older siblings exposed to the cue of seeing their mother care for a younger sibling as a newborn reported intense levels of disgust toward sexual acts with that sibling as well as increased levels of altruism across all durations of coresidence. Regardless of whether a subject resided for fifteen or only three years with their younger sibling, the level of sexual aversion reported in response to sibling incest and altruistic inclinations were close to the maximum. In contrast, for subjects for whom this cue was not available and who relied on coresidence duration as a cue to siblingship (the younger siblings in the dataset), disgust at sexual acts with their older sibling and sibling-directed altruism were low for shorter periods of coresidence and gradually increased with extended periods of coresidence. Data suggest it takes approximately fourteen to fifteen years of coresidence for younger siblings to reach the same level of sexual aversions and altruistic effort reported by older siblings who were exposed to the cue of seeing their mother care for their sibling as a newborn.

Taken together, these data provide a first glimpse into the cognitive procedures governing kin detection and kin-directed behavior in humans. The findings indicate that the mind uses at least two cues to detect siblings and mediate inbreeding avoidance and kin-directed altruism: exposure to maternal investments in a newborn (used by older siblings to detect younger siblings) and duration of coresidence throughout periods of shared parental investment (typically used by younger siblings to detect older siblings). Because these same cues were found to regulate aversions and altruism in the same way, it suggests the existence of a single set of kinship-estimating procedures that feed motivational systems guiding mate choice and, separately, altruistic effort.

Cues aside from coresidence duration and exposure to maternal-infant association may also play a role in sibling detection. For example, facial resemblance has been found to predict trustworthiness (DeBruine, 2005) and olfactory cues such as those derived from the major histocompatibility complex (MHC) have been found to influence mate choice (e.g., Wedekind & Füri, 1997).

While intriguing, there are reasons to remain suspect about humans' usage of facial resemblance and MHC as kinship cues. With respect to facial resemblance, siblings may have happened to inherit, by a roll of the dice, many or just a few of the same alleles that generate facial phenotypes. If kin-detection systems relied only on these cues, they would likely estimate in error the average similarity across the entire genome. Why privilege the face? If this argument isn't compelling, then consider the fact that ancestral humans would have had little idea of what they looked like—there were no mirrors in the Environment of Evolutionary Adaptedness.

But the patterns found between assessments of similarity (facial, attitudinal, earlobe, or otherwise) and trustworthiness still need to be explained (we would argue that the evidence regarding attraction is thin and not worth addressing here). An alternate explanation for why similarity enhances altruism and liking is that a sign of commonality can indicate who might be a candidate for a relationship based on mutual value. If you and I are similar, there is a chance we might value one another for this similarity and a chance we might be similar in other ways. Similarity opens the door to friendships. If true, dissimilarity should close it. Evidence suggests this is indeed the case (Lieberman et al., 2022). Last, with respect to MHC we note that MHC similarity may not function as a cue to kinship per se but rather might be taken as input by the system assessing another person's expected fitness value as a sexual partner (see below) to assess genetic compatibility. A person who shares similar MHC alleles is not an optimal mate, kin or not.

AUNTS, UNCLES, COUSINS, NIECES, AND NEPHEWS

As mentioned earlier, as one moves further out on the family tree, the negative effects of inbreeding drop off. Nevertheless, they are still present, suggesting that somehow the mind computes the relatedness of nonnuclear family members. One way this can occur is via transmitted information. As an anecdote, when Deb's (the first author's) son was little, he went through a stage in which he incessantly asked about all the family relationships "How are you related to Aunt Amy? Did you have the same mom? And Pop-pop is both your dad?; But Aunt Jackie has a different mom and dad?" Despite not living with Amy or Jackie or seeing them regularly, Deb's son was piecing together the fact that she had a sister who was related and a sister who was not. These questions were repeated several times over the course of a few months suggesting the provocative possibility that the mind initiates a program early in development for verifying one's family tree and social relationships of close others. The cognitive development of explicit kin relations is an area of important research

in which there is much to discover.

Facets of Mate Choice

Kinship cues on their own buy little behavior. To avoid inbreeding, estimates of kinship that result from the detection of kinship cues need to somehow influence sexual motivations. As detailed in Lieberman and Patrick (2018), one way this occurs is depicted in figure 8.1. Kinship, while certainly an important factor, is not the only factor that affected the lifetime reproductive success of a given individual. Instead, kinship is likely traded off against the other dimensions that reliably generated variation in offspring survivability in ancestral environments. These dimensions include, but are not limited to, the mate value of a given individual, one's perceptions of one's own mate value, mate availability, and local norms threatening condemnation.

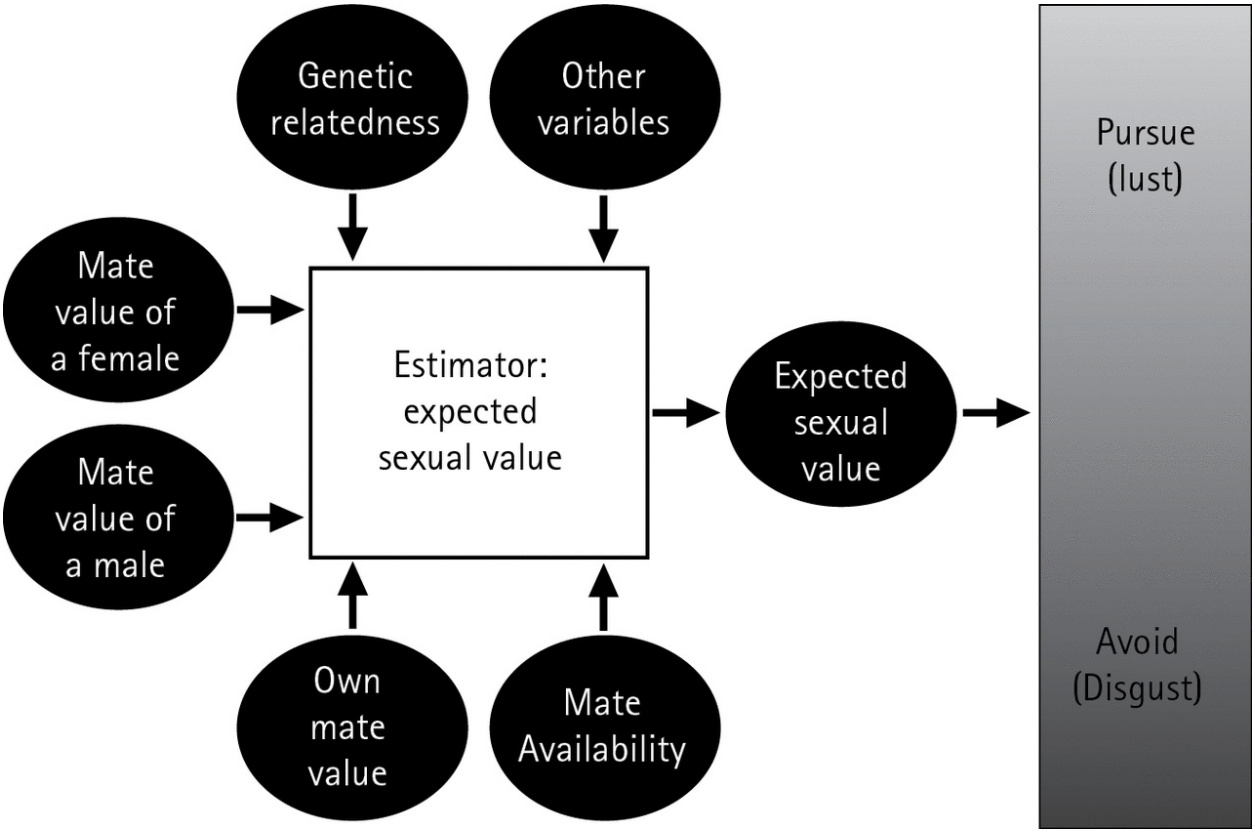

Figure 8.1 Inputs for a sexual motivation system.

As shown in figure 8.1, estimates of each dimension listed above are taken as input by a system that computes a variable we term "expected sexual value" (Tybur et al., 2013). The *expected sexual value* of another individual registers the

reproductive gains (or losses) associated with selecting him or her as a sexual partner *for oneself*. We briefly walk through each dimension that contributes to the estimation of expected sexual value to illustrate how relatedness is traded off in the generation of sexual motivations before returning to the emotion of disgust. We note that this is just one potential design of a mate choice system (see also Conroy-Beam, 2021).

ANOTHER'S MATE VALUE

As discussed by several evolutionary minded scientists (e.g., Buss, 2003; Miller, 2001), for men, mate value is typically a function of (1) cues indicative of a developmental body plan robust against genetic and pathogenic threats, (2) his ability to obtain and defend resources, and (3) willingness to share said resources with a female and her offspring. For females, mate value is typically a function of (1) cues indicative of a developmental body plan robust against genetic and pathogenic threats and (2) cues to fertility.

Practically speaking, our ability to assign mate value to another individual depends first on the ability to categorize a person as male or female, and second on the application of gender-specific mate value criteria. Arguably, for heterosexual psychologies, the mate value of opposite-sex individuals are weighted more positively than the mate value of same sex individuals when it comes to decisions to pursue another individual as a sexual partner. The opposite holds for homosexual psychologies. Thus, despite both men and women being able to compute the mate value for a given male, the computed mate value will tend to decrease the expected sexual value of the male for men and (could potentially) increase the expected sexual value of the male for women. Of course, assessments of mate value can serve as inputs to systems beyond those making decisions regarding the suitability of a given individual as a sexual partner for oneself. For instance, they can be used to assess possibilities of mate poaching and other forms of intrasexual competition.

Regardless, our main point is that kinship is, generally, traded off against mate value. One's sibling or parent might yield high mate value estimates, yet an elevated estimate of kinship overrides sexual motivations that might otherwise ensue.

ONE'S OWN MATE VALUE

Another dimension that would have influenced mate choice and outcomes is one's perceptions of one's own mate value (Arnocky, 2018; Buss & Shackelford, 2008). In the absence of mirrors, our ancestors would have had to form an idea of how they rated in terms of their attractiveness, particularly their facial

attractiveness, by the feedback they received from others in the environment. The frequency with which others made eye contact versus looked away, smiled versus frowned, approached versus avoided, or delivered benefits (such as gifts) versus imposed costs (such as physical harm) would have enabled both men and women to make inferences regarding their own mate value and the quality of mate they might be able to expect. By and large, a female at the top of the mate-value scale has the leverage to obtain a male with correspondingly high mate value. All other things being equal, a female at the lower end of the mate-value scale does not.

Recent studies on mate preferences lend support to the idea that one's own mate value factors into perceptions of attractiveness. For instance, Morgan and Kisley (2014) manipulated males' sense of their own attractiveness via feedback and then presented them with attractive and unattractive faces. All males attended to attractive faces, regardless of whether they were given feedback that they were of high or low market value. But males told they were of high market value spent significantly *less* time attending to unattractive faces as compared to males told they were of low market value. Similarly, Yong and Li (2012) had both men and women hold a small sum (~$84) or large sum (~$2,100) of money and found that men—but not the women—who held the large sum of money *increased* their minimum requirements in the attractiveness of a potential date. For females, Buss and Shackelford (2008) found that more physically attractive women held higher standards for an acceptable mate in terms of his masculinity, income, desire for a home and children, and devotion as a partner. Thus, both sexes appear to use information of their own mate value to guide their sexual pursuits.

MATE AVAILABILITY

Mate availability too is a dimension that should update decisions about who to pursue as a sexual partner. A general prediction is that the more restricted the perceived mating pool, the more relaxed one's preferences. Evidence of this comes from the list of risk factors that contribute to child abuse and neglect. Of course, given the sex differences in parental investment, women should be more reticent to relax mate preferences as compared to men. Indeed, women tend to find all manner of sexual behaviors, including incest, far more objectionable than do men (Lieberman et al., 2007; Tybur et al., 2009). Our main point here is that context will influence the sexual value assigned to a given individual.

OTHER VARIABLES

No doubt there are other dimensions that impinge upon the assessment of the

sexual value of another individual. One omitted from figure 8.1 is the internalization of social norms condemning the selection of particular individuals as sexual partners. Whereas an individual might not be kin, might register as having a high mate value, and might be within striking distance given one's own mate value, norms and laws that forbid selection can render an otherwise desirable mate as one to be avoided. Likewise, exposure and experience play roles in calibrating disgust systems—sexual, tactile, or consumptive. Thus, additional inputs that relate the likelihood of punishment and past experiences cannot be ignored in any model of mate choice and sexual motivation.

Sexual Value and Disgust

According to the model of mate choice/inbreeding avoidance we posit—again, just a back-of-the-napkin snapshot of how a sexual motivation system might be engineered—the computed *expected sexual value* of an individual is their assessed sexual attractiveness and sets in motion the constellation of muscle movements and cognitive systems that were retained due to their positive effects on their replication down the generations. When positive and elevated, *expected sexual value* triggers sexual pursuit (lust); when negative and low, it triggers sexual avoidance (disgust). A low sexual value can result from several inputs, but of relevance here, a high estimate of genetic relatedness will lead to a very low expected sexual value and will trigger sexual avoidance when sexual motives are detected. Of course, genetic relatedness will be traded off against other factors that statistically affected reproductive success over the course of human evolution. For women, given the additional costs of producing an offspring with a better than average chance of suffering higher mortality and disease, the sexual value of a close male relative is likely to remain low compared to the sexual value for other males. But for men, who have far lower levels of parental investment, opportunities to increase reproductive success through inbreeding might seem less objectionable, all things considered. That is, we should see different thresholds associated with incest avoidance adaptations.

The emotion proposed to govern sexual avoidance is disgust, which was a felicitous system for natural selection to co-opt for this purpose. This is because disgust is already linked to sex (see Tybur et al., 2013). Initiation of sexual contact requires the suspension of systems that motivate the avoidance of pathogens. If instead of being lowered, disgust was raised in response to particular cues (e.g., genetic relatedness and low mate value), natural selection would well be in its way to engineering a sexual-avoidance system. Other

readings (e.g., Lieberman & Patrick, 2018; Rozin et al., 2008; Tybur et al., 2013) provide a longer discussion of the emotion disgust, its evolved functions, and myriad elicitors.

Conclusion

In sum, inbreeding avoidance systems are part of the larger mate choice system. Sexual reproduction, as an adaptation for generating rare genotypes to which pathogens are less well acclimated, includes mental subroutines for identifying more similar genotypes and avoiding them as partners. In terms of the information-processing structure of mate choice adaptations, we advance a model in which the mind computes the sexual value of other individuals and regulates motivations to pursue or avoid them accordingly. In addition to mate value and genetic relatedness, the mind likely weighs the availability of mates and one's own mate value in the assessment of how sexually attractive another person is for oneself. Whereas high magnitudes of expected sexual value activate lust and sexual motivations to pursue another as a sexual partner, low computed magnitudes of expected sexual value activate disgust and motivations to avoid another as a sexual partner. Applying an evolutionary framework to understanding these systems has led to recent advances, but there is certainly far more work to be done.

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CHAPTER
9

Parental Influence over Mate Choice

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Abstract

Across different cultures and times, parents exercise considerable influence over their children's mating decisions. This chapter examines why and how parents influence mate choice, and the evolutionary implications of such influence. In particular, it will be argued that, from the perspective of parents, there is an opportunity cost arising from allowing children to exercise mate choice on their own, which motivates parents to influence mate choice in order to reduce it. In the preindustrial context, parents influenced mate choice more directly, through social institutions such as arranged marriage, which is examined in detail. In postindustrial societies, such as the United States, parents exercise influence indirectly through manipulation, and this chapter examines the manipulation tactics they employ. There are reasons to believe that parental influence has been strong for the greatest part of human evolution, which is likely to have affected the evolutionary trajectory of several mechanisms or adaptations involved in mating. The present chapter discusses some of these adaptations and how they have been affected by the transition to the postindustrial environment, where parental influence over mating is much weaker.

Key Words: parental influence over mating, parent-offspring conflict, parental control, arranged marriage, parental choice

Across different cultures and different times, parents exercise considerable influence over their children's mate choices (Apostolou, 2007b, 2010, 2012). In the current chapter, I examine the nature of this influence and how it is manifested in different cultural settings. I also examine parental influence in

ancestral human societies, as well as its evolutionary implications.

Why Parents Influence Mate Choice

Children exercising mate choice freely entails an opportunity cost for their parents, which motivates the latter to control the mate choices of the former. Accordingly, in the current section I will examine the opportunity cost of free mate choice and its components.

The Converging Opportunity Cost of Free Mate Choice

Bodies consist of adaptations which have evolved to propagate the genes that code for them in future generations (Dawkins, 2018). Adaptations do so by enabling individuals to survive and/or reproduce. For instance, some genes move to future generations by coding for a brain mechanism, which generates the feeling of hunger when the body's energy reserves start running out. Hunger is an unpleasant feeling, and in order to get rid of it, people are motivated to find and eat food. By doing so, they increase their chances to survive, which in turn, increases the chances of the genes that code for this mechanism to pass to future generations. In this respect, organisms can be understood to behave *as if* maximizing their survival and reproductive success—that is, the chances to pass their genetic material to future generations termed fitness (Dawkins, 2018).

Copies of a gene are spread across bodies of genetic relatives. For instance, if an individual carries a specific gene, there is a 50 percent chance that its siblings also carry the same gene. Accordingly, genes may propagate to future generations by coding for mechanisms that motivate individuals who carry them to assist their genetic relatives who are also likely to carry them (Hamilton, 1964). For example, genes may code for a mechanism that makes an individual love its siblings. This emotion will motivate the individual to assists its brothers and sisters in their survival and reproductive effort, which will increase the chances that the genes that code for this mechanism are represented in future generations. In this respect, individual organisms can be understood to behave *as if* maximizing their inclusive fitness—that is, their own plus their genetic relatives' survival and reproductive success (Dawkins, 2018; Hamilton, 1964).

The more closely genetically related two individuals are, the higher the chances are that they carry a copy of a specific gene. For instance, the chances that an individual carries a specific gene are 100 percent, that its sibling carries it 50 percent, and that its cousin carries it 12.5 percent. This logic mandates that genetic relatives have both converging and diverging genetic interests, which in

turn, means that they would maximize their inclusive fitness by assisting each other with their survival and reproductive success, with the assistance increasing proportionally to the strength of the genetic relationship.

A parent and its child share 50 percent of their genes and consequently have substantial converging genetic interests. An area where converging interests are manifested is mating: if the child is successful in attracting a good mate and procreates, its parent's fitness increases considerably as its genes pass to future generations. Accordingly, the parent has vested interests in its child being successful in its mating effort and is likely to assist it in being so. For instance, the parent may finance a plastic surgery or the purchase of a fancy car, making the child more appealing as a mate.

The parent may also attempt to influence its child toward making more optimal mate choices. In particular, mating involves considerable deception (Haselton et al., 2005). For instance, in the disguise of true interest in a long-term relationship, individuals may approach a mate only to extract short-term benefits, such as money. Furthermore, in order to attract desirable mates, people may exaggerate their good qualities and hide their undesirable ones. For example, a man may be dressed with fancy clothes and drive an expensive car in order to signal wealth and high social status, traits which are valued by women in a partner (Buss, 2016). Yet, he may actually be poor and unsuccessful, having spent all his money in clothing and borrowed or rented the car.

Mate-seekers are usually young, lacking experience in mating, while they base their mating decisions on emotions such as romantic love and high libido. High libido and intense feelings of love may distort judgment and, along with limited experience, make mate-seekers vulnerable to deception. On the other hand, their parents are usually more experienced in mating, and when assessing prospective mates for their children, their judgment is not impaired by libido and romantic love. In effect, if they choose to interfere, parents have the capacity to protect their children from making erroneous mate choices (Apostolou, 2016a).

Opportunity cost is the cost of inaction: what individuals lose by not performing a specific action and performing an alternative one (Buchanan, 1991). In the case of mating, if parents do not influence their children's mate choices and leave them instead to exercise choice freely, they will potentially suffer a fitness cost arising from their children's poor mating decisions. This cost could be called converging opportunity cost of mate choice, because parents' and children's interest converge in the latter not making erroneous mate choices (Apostolou, 2016a, 2017b). The presence of the converging opportunity cost would motivate parents to influence their daughters' and sons' mate choices in order to reduce it.

The Diverging Opportunity Cost of Free Mate Choice

A parent and its child do not share 50 percent of their genes, which means that their genetic interests diverge. Mating is one domain where divergence of genetic interests and possible conflict is manifested (Apostolou, 2008a; Trivers, 1974). More specifically, people look for mates who have traits likely to increase the chances that their genetic material is represented in future generations. For instance, prospective mates differ in their genetic quality: Some carry genes that enable them to better resist the challenges of the environment, while others carry genes that do not. By having a mate of good genetic quality, a mate-seeker would have children who are also likely to carry these good genes and thus have better chances of passing the mate-seeker's genes to future generations. By having an in-law of good genetic quality, a parent would have grandchildren who are also likely to carry these good genes and, as a consequence, better chances of passing the parent's genes to future generations.

The fitness benefits of a given trait translate into selection pressures to favor adaptations that would enable individuals to attract mates and in-laws who have desirable qualities. Mate and in-law preferences constitute such mechanisms: People tend to prefer fitness-increasing traits in prospective mates and in-laws, which enable them to divert their limited resources in attracting individuals who have these qualities, and avoid those who do not (Apostolou, 2007a; Buss, 1989). Returning to our example, research has found that people tend to prefer good genetic quality proxied by good looks (Gangestad et al., 1994; Thornhill & Gangestad, 1993) in prospective mates and in-laws (Apostolou, 2007a; Buss, 1989, 2016; Wang & Apostolou, 2017).

Nevertheless, the benefit that parents and children derive from good genetic quality is not the same. More specifically, by attracting a mate with good genetic quality, a mate-seeker increases the chances that 50 percent of its genes pass to future generations, which constitute however, 25 percent of its parent's genes. Therefore, *ceteris paribus*, the fitness benefit that the parent would derive from the good genetic quality of an in-law would be half the benefit that its child (i.e., the mate-seeker) would derive from a mate. It follows that selection forces would have adjusted preferences so that good genetic quality is preferred more in an in-law than in a mate (Apostolou, 2008a).

In order to test this prediction, I asked parents to rate how desirable they considered a set of traits, including good looks, in a prospective mate for themselves and in a prospective mate for their children (Apostolou, 2008a, 2008b). I found that participants indicated a stronger preference for good looks in a prospective mate than in a prospective in-law. Another set of studies asked

parents to rate several traits, including good looks, in a prospective partner for their children and their children to rate the same traits in a prospective partner for themselves. Comparisons of scores between the two parties indicated that parents gave significantly lower scores to good looks than their children (Apostolou, 2015a; Apostolou & Wang, 2018; Fugère et al., 2017; Guo et al., 2017; Perilloux et al., 2011). Using different methodologies, other studies have found that good looks are valued more in a mate than in an in-law (Bovet et al., 2018; Buunk et al., 2008; Buunk & Solano, 2010; Dubbs & Buunk, 2010; Dubbs et al., 2013; Lefevre & Saxton, 2017).

In-law and mate preferences also diverge in regard to family background. In more detail, evidence from historical and contemporary preindustrial societies indicates that parents employ the marriages of their children in order to make beneficial alliances with other families (Apostolou, 2014). Such alliances could provide considerable material and nonmaterial benefits to parents and their relatives, including their children. However, children in preindustrial societies do not appear to use their mating decisions in order to forge alliances with other families. One likely reason is that, due to parental control over mating, children have limited space to negotiate their own marriages. Thus, it would pay parents to sensitive to the family background of prospective in-laws in order to make more sound alliances. On the other hand, children would not place such emphasis, as alliances are not the primary objective of their mating decisions. This argument would predict that parents would prefer good family background more in a prospective in-law than their children would prefer it in a mate, which appears to be the case (Apostolou, 2008b; Apostolou & Wang, 2018). Disagreement is not confined only to good looks and family background, with research indicating that traits such as being cheerful are preferred more in a spouse than in an in-law, while others such as similar religious and ethnic background are preferred more in an in-law than in a spouse (Apostolou, 2015a; Apostolou et al., 2014; Apostolou & Wang, 2018; Perilloux et al., 2011).

Divergence in preferences does not necessarily lead to conflict. For instance, even if parents ascribe less importance to the good looks of a prospective in-law, they will not be dissatisfied if their children manage to secure good-looking mates as they are also going to derive inclusive fitness benefits from this trait. They are likely, however, to be dissatisfied with the compromises in other traits that their children have made in order to get a good-looking mate. In more detail, mate-seekers are constrained by their own mate value in the mate value of mates they can attract, one reason being that individuals are unwilling to settle with long-term mates of lower value than their own mate value. Consequently, people need to settle with mates of a value similar to their own mate value, and with the

exception of the extremely rare scenario that they score top in all traits, in order to do so, they have to compromise regarding some traits (Luo, 2017).

The trade-offs mate-seekers would make depend on the fitness they derive from each trait; for instance, they would be less willing to trade a high fitness-increasing than a low fitness-increasing trait. Yet, because traits such as good genetic quality give different fitness benefits to children and to parents, the trade-offs that children would make would not be considered optimal by their parents. For example, children may compromise considerably on traits such as good social standing in order to get more good looks. Assuming that both parties gain the same from good social standing, parents who do not gain as much from good genetic quality would consider such trade-off not to be fitness-maximizing. If they were to exercise choice for their children, they would compromise less on good social standing and more on good looks. In this respect, parents would not disagree with their children bringing home good-looking mates but with the compromises their children did in order to do so.

I have examined this argument theoretically (Apostolou, 2017b), and tested it empirically (Apostolou, 2011). In one study, I asked parents and their children to allocate a fixed number of mate points to several traits in a prospective spouse for themselves and in a prospective spouse for their children (Apostolou, 2011). I found that children would allocate more points to good looks, spending less on traits such as good family background, in comparison to their parents who allocated fewer points to good looks and more to good family background. Consequently, children's mate choices would be costly to their parents in terms of good family background and other desirable traits, which cannot be compensated by gains in good looks, which are less valuable to them.

In sum, different traits give different benefits to parents and their children, which has resulted in divergence in in-law and mate preferences, driving each party to make different compromises when exercising in-law and mate choice respectively. Consequently, children's free mate choice involves an opportunity cost for parents, which equals to the traits they would get if they were to exercise choice for their children, and they do not because their children exercise choice on their own. This opportunity cost could be called divergent as it arises from divergent genetic interests between parents and children (Apostolou, 2016a, 2017b). The divergent opportunity cost would motivate parents to exercise influence over their children's mating decisions in order to reduce it.

DAUGHTERS AND SONS

Children exercising mate choice totally independently from the influence of their parents involves a considerable opportunity cost for the latter, which

consists of the converging and the diverging opportunity costs. This cost is usually higher for daughters than for sons (Apostolou, 2016a, 2017b). More specifically, because men do not have to bear the costs of pregnancy, they gain more fitness benefits from opportunistic sex than women (Buss & Schmitt, 1993, 2019). As a consequence, they are more likely to employ deception, presenting themselves, for instance, as having an interest in a long-term relationship while they only care for casual sex (Haselton et al., 2005). If such strategies lead to pregnancy, they could be detrimental for the fitness of women and their parents, who have to raise the child without paternal support. Moreover, across cultures, men value sexual restraint in women (Buss, 1989), while in many preindustrial societies virginity is a prerequisite for a marriage to proceed, and parents who do not manage to keep their daughters virgin suffer considerable social status loss (Apostolou, 2014; Campbell, 1964). Therefore, even if these strategies do not lead to pregnancy, they could also involve substantial fitness losses for women and their parents. Accordingly, parents have more to lose if they fail to influence their daughters' than their sons' mate choices in avoiding to make erroneous mate choices. In short, the converging opportunity cost of free mate choice is higher for daughters than for sons.

Pregnancy in our species usually takes nine months, and following birth, women breastfeed their children for several months. Thus, a sexual contact that leads to pregnancy would prevent a woman from having another child for more than a year. On the other hand, following such an event, a man could be ready to fertilize another women in less than an hour. In effect, at any given point in time, more men than women are available in the mating market, and due to the law of demand and supply, women have a higher mate value than men. It follows that daughters are more valuable than sons as a reproductive resource, meaning that parents can extract more benefits by influencing their daughter's than their son's mate choices. To put it differently, parents have potentially more to lose if they allow their daughters rather than their sons to exercise mate choice freely, which means that the diverging opportunity cost of free mate choices is higher for the former than for the latter (Apostolou, 2016a).

Furthermore, women are on average physically weaker than men, which makes them more vulnerable to external threats such as the risk of being raped (see also Apostolou, 2013c; Buss, 2021; Perilloux et al., 2011). Consequently, daughters are more dependent on their family for protection than sons, and parents can use this dependence in order to influence mate choice. In addition, it is easier for parents to impose their will by means of physical force on their daughters than on their sons. That is, it is easier for parents to influence their daughter's than their son's mate choices; thus, *ceteris paribus*, in order to

achieve the same outcome (i.e., to influence a specific mate choice), parents have to allocate fewer resources in doing so for their daughters than in doing so for their sons. In effect, parents can potentially gain the same fitness benefit at a lower cost in the case of their daughters; the net benefit (i.e., the benefit minus the cost) would be higher for influencing daughters than sons. Overall, parents have more to lose if they allow their daughters rather than their sons to exercise choice freely. In sum, the asymmetry in physical strength between daughters and sons results in higher opportunity cost of free mate choice for daughters than for sons (Apostolou, 2016a, 2017b).

This asymmetry results in an asymmetry in both the converging and the diverging opportunity costs: It is easier for parents to influence their daughters rather than their sons in not making an erroneous choice, and it is easier to influence their daughters rather than their sons in making a mate choice which is optimal for parents. Overall, the opportunity cost of free mate choice is higher for daughters than for sons, which leads to the prediction that parents would be more strongly motivated to influence their daughters' than their sons' mate choices.

MOTHERS AND FATHERS

The opportunity cost of free mate choice does not vary only with the sex of the offspring but also with the sex of the parent. More specifically, fathers are on average physically stronger than mothers, while across human societies, men tend to control more wealth and have higher social status than do women in most or all cultures (Goldberg, 1993). These differences indicate that children would be more dependent on their fathers for resources and protection, while it would be easier for the latter to impose their will on the former through physical force. Accordingly, the total opportunity cost of free mate choice would be higher for fathers than for mothers (Apostolou, 2016a, 2017b).

Because men gain more reproductive benefits than women from having sex with different partners, and because attracting mates requires resources, fathers could potentially derive more reproductive benefits than mothers from influencing their children's mate choices. For instance, across preindustrial societies, polygyny and bride wealth are commonly practiced (Goody & Tambiah, 1973). Polygyny allows a man to have more than one wife, while in the institution of bride wealth, a man has to collect a considerable amount of wealth which he pays to the father of his prospective wife (Goody & Tambiah, 1973). Thus, a father could give his daughter to a man who lacks several desirable traits, such as good looks and young age, but who is willing to pay a high bride wealth. He could subsequently use this bride wealth in order to secure

another wife for himself and have more children with her. Such action is not optimal for his daughter, however, who faces a reduction in her chance to have offspring with good chances of survival and reproduction, and with whom, she is more closely genetically related than with her half-siblings.

Furthermore, women give birth to their children, while men do not. From this fact, it follows that women are certain that the children they give birth to are their own, while men are not certain that the children their partners give birth to are their own. Accordingly, the fathers but not the mothers will discount the degree of genetic relatedness to their children by the probability that they are not actually their own. In effect, there would be more divergence in the genetic interests between fathers and their children than mothers and their children, and thus, the diverging opportunity cost would be higher for fathers than for mothers (Apostolou, 2016a, 2017b). A father would be more willing than a mother to give his daughter to an old man in return for a high bride wealth or the reciprocal bestowal of a daughter on him from that old man, not only because he could derive more reproductive benefits from it but because the cost of doing so (i.e., his daughter being mated with a man of limited reproductive potential) is lower as there is the possibility that she is not actually his daughter. On the other hand, the converging opportunity cost would be higher for mothers than for fathers. For instance, if children make a fitness-impairing mate choice, the fitness of mothers would be impaired more than the fitness of fathers, as the latter would discount the decrease in fitness by the probability that their children are not their own. Overall, due to paternal uncertainty, the diverging opportunity cost of free mate choice would be higher for fathers than for mothers, while the converging opportunity cost would be higher for mothers than for fathers (Apostolou, 2016a, 2017b).

In sum, we expect that the opportunity cost of free mate choice would be usually higher for fathers than for mothers, which predicts that fathers would exercise more influence over their children's mating decisions than mothers. In addition, because the opportunity cost of free mate choice is higher for daughters than for sons, a common pattern would be for fathers to exercise influence over their daughters' mating behavior. I use the term "usually" because the opportunity cost of free mate choice, and thus parental influence, could be affected by different situational factors. For instance, a war may result in a considerable shortage of men, which would increase the mate value of sons and decrease the mate value of daughters, and could result in parents attempting to influence more their sons' than their daughters' mate choices.

Parental Influence over Mate Choice across Human Societies

The opportunity cost of free mate choice gives a strong incentive to parents to influence their children's mate choices. Accordingly, in the current section I will examine parental influence over mating in different societies.

Preindustrial Societies

Based on their subsistence, preindustrial societies could be divided in two broad categories: hunting and gathering and agropastoral. Hunters and gatherers live in small groups of fifty to one hundred fifty individuals, are not sedentary, and base their subsistence on gathering plants and hunting animals (Lee & Devore, 1968). Agropastoralists live in larger communities, are sedentary, and base their subsistence on farming the land and herding animals (Bocquet-Appel, 2011). In preindustrial societies, individuals, especially women, are married soon after they reach sexual maturity, so reproduction takes place predominantly within the institution of marriage. Arranged marriage is practiced, which constitutes a manifestation of direct parental control over mating (Apostolou, 2013b). More specifically, in this institution parents and other relatives negotiate the marriage of their children with parents and relatives of another family. The consent of the children is frequently asked, but it is usually not necessary for the marriage to proceed (Apostolou, 2014).

HUNTING AND GATHERING SOCIETIES

In order to examine parental influence in this context, I coded anthropological data from a sample of 190 contemporary hunting and gathering societies (Apostolou, 2007b). I found that, in approximately 70 percent of the cases, marriages were arranged, whereas in about 18 percent of the cases marriage was arranged by relatives other than parents, in about 8 percent of the cases children found their own spouses but their choices were subject to their parents' approval, and finally, children found spouses independently of their parents' will was reported in about 4 percent of the cases.

In marriage negotiations, fathers had usually a primary role. More specifically, in about 44 percent of societies, fathers and other male relatives arranged the marriages of their children, with little input from mothers and other female relatives. Furthermore, in about 16 percent of the societies fathers dominated arrangements but mothers had an important say, in about 34 percent of the societies both fathers and mothers had a roughly equal contribution, and in about 8 percent of the societies both parties contributed but mothers dominated the arrangements.

I have also examined mating patterns by analyzing coded data for first marriage from the Standard Cross-Cultural Sample (SCCS) (Apostolou, 2010). The SCCS is a sample of 186 preindustrial societies which are relatively independent from each other (Murdock & White, 1980). I found that, for women, in approximately 53 percent of the societies, marriage was arranged, and in approximately 8 percent of the societies it was based on free mate choice, with the respective percentages for men being 31 percent and 40 percent. Finally, in about 18 percent of the cases, fathers and other male relatives such as uncles and brothers monopolized marriage arrangements, in about 23.5 percent both parties contributed but fathers had more say, in about 47 percent both parties had roughly an equal say, and in about 12 percent both parties participated but mothers had more say.

AGROPASTORAL SOCIETIES

In order to examine mating patterns in the agropastoral context, I employed precoded data on first marriage from the SCCS (Apostolou, 2010). In this setting, similarly to the hunting and gathering one, arranged marriage was the most prevalent type of marriage. In more detail, in societies that based their subsistence predominantly on agriculture, for women, arranged marriage was the most frequent mode of long-term mating in 40.3 percent of the cases, followed by courtship subject to parental approval in 28.1 percent, arranged marriage and free courtship marriage both practiced in 24.5 percent, and courtship marriage in 7 percent of the cases. For men, the rates were 30.4 percent, 23.2 percent, 23.2 percent, and 23.2 percent, respectively. In societies that based their subsistence predominantly on animal husbandry, for women, arranged marriage was practiced in 72.7 percent, courtship subject to parental approval in 18.2 percent, and both arranged marriage and courtship in 9.1 percent of the cases, whereas there was no case where marriage was based predominantly on courtship. For men, the respective ratings were 41.7 percent, 25 percent, and 16.7 percent, whereas in 16.7 percent of the cases marriage was based on free courtship. In societies that based their subsistence on a combination of agriculture and animal husbandry, for women, in approximately 53 percent of the cases, marriages were arranged; in 21 percent, marriages were either arranged or free choice in 16 percent, marriages were based on courtship subject to parental approval; and in approximately 10 percent of the cases, they were based on free mate choice, with the respective rates for men being 39 percent, 17 percent, 11 percent, and 33 percent.

Parental control over mating was stronger over daughters than over sons. More specifically, in societies where subsistence was based predominantly on

agriculture, for women, in approximately 40 percent of the cases, marriages were arranged, while for men the respective rate was 30 percent. In the same vein, in societies where subsistence was based predominantly on animal husbandry, for women, in approximately 73 percent of the cases, marriages were arranged, while the respective rate for men was 42 percent. Moreover, in societies where subsistence was based on a combination of agriculture and animal husbandry, for women, in approximately 53 percent of the cases, marriages were arranged, while the respective rate for men was 39 percent.

Fathers had a greater influence than mothers over marriage arrangements. In particular, in societies that based their subsistence predominantly on agriculture, in 25 percent of the cases, men monopolized marriage arrangements, in approximately 39 percent of the cases both parents participated but men had more say, in 22 percent fathers and mothers had an equal say, and in 14 percent of the cases both parents participated but mothers had more say. In societies that based their subsistence predominantly on animal husbandry, in 71 percent of the cases, both parents participated in marriage arrangements but fathers had more say, and in 29 percent of the cases both participated with roughly equal say. In societies that based their subsistence on both agriculture and animal husbandry, in 80 percent of the cases, both parents participated but men had more say, in 10 percent men dominated marriage arrangements, and in 10 percent of the cases both parents had an equal say. Finally, there was no case reported where mothers dominated marriage arrangements.

In a different study, I coded historical data for sixteen agropastoral societies, such as Classical Greece and Imperial China, spanning a time period of about five thousand years (Apostolou, 2012). I found that in fifteen societies, first and later marriages were arranged, while for one society the historical records were not clear about which was the typical form of marriage. I found also that in 90 percent of the cases, parents exercised more control over their daughters' than over their sons' mating decisions, and only in 10 percent of the cases both sexes were equally controlled. There was no case reported where parents exercised more control over their sons than over their daughters. In addition, in ten societies marriages were predominantly controlled by fathers, while in four societies both parents participated but fathers had more say. Finally, there was no case reported where women had more say, or where they dominated marriage arrangements.

MATING CONTROL INSTITUTIONS

In preindustrial societies, lacking individual rights protection systems, parents frequently employ more aggressive ways to control their children's and

especially their daughters' mate choices. These practices and customs, which are associated with restricting and regulating mating behavior, could be collectively called mating control institutions, and they take different forms in different cultural contexts (Apostolou, 2013b). One such institution is female circumcision, which is practiced in many preindustrial societies. Here, when they reach sexual maturity, girls undergo a procedure in which their clitoris is removed (Gruenbaum, 2001). In this way, their capacity to experience sexual pleasure diminishes, and they are less likely to seek mates and more likely to stay within their parents' control. A less frequent type of female circumcision is infibulation, which takes place before puberty and involves the sewing of the labia majora together, allowing only a small opening for urination (Gregersen, 1982; Lowenfels, 1977).

Foot binding is another custom practiced for more than ten centuries in China (Mackie 1996; Ping, 2002). Here, the mother or another female relative binds her daughter's feet when she is four or five years old and sometimes younger (Jackson, 1997). This procedure involves each of the toes to be broken and pressed under the sole of the foot. Following that, the arches of the feet are also broken, and the broken feet are bound tightly with the toes folded under the sole of the foot (Jackson, 1997; Ping, 2002). The consequence of this procedure is for women's feet to remain small and their walking to be severely impaired, making them more dependent on their family and later on their husbands (Jackson, 1997; Ko, 2007).

Is parental influence total?

The anthropological and historical evidence discussed above indicates that in the preindustrial context, parents exercise considerable influence over their children's mating decisions. This evidence raises the question of whether parental influence is absolute, with children lacking any space to exercise choice. The answer is that parental influence is not absolute, and children have substantial space to exercise choice. More specifically, children can exercise choice within marriage in establishing relationships with extra-pair partners of their own choice, or sex partners prior to marriage. In addition, children can elope or run away with a loved one or divorce the partners their parents have selected for them, but subsequent marriages are usually also arranged. Furthermore, in several societies, marriage based on courtship is considered acceptable, especially if parents approve their children's partners. Similarly, children can use psychological manipulation in order to persuade their parents not to marry them with undesirable mates or to marry them with desirable ones.

Last but not least, in order to establish more long-lasting marriages, when they arrange a marriage, parents implicitly or explicitly take into consideration their children's mate preferences (Apostolou, 2017a; see also 6).

Parental influence in ancestral human societies

The anthropological and historical evidence discussed previously can enable us to make valid inferences about parental influence in ancestral human societies. The genus *Homo* appeared on earth approximately two million years ago, and until approximately ten thousand years ago and the onset of agropastoral revolution, our ancestors lived as hunters and gatherers (Lee & Devore, 1968). The way of life of contemporary hunters and gathers is most likely very similar to the way of life of ancestral ones, so the patterns of mating anthropologists have observed in the former are likely to have been present in the latter (Lee & Devore, 1968). On this basis, it could be argued that strong parental control over mating, with parents exercising more influence than mothers and parents controlling more their daughters than their sons, characterized the period of human evolution up to the onset of the agropastoral revolution.

Following the agropastoral revolution, human societies started shifting their subsistence from hunting and gathering to cultivating land and herding animals (Bocquet-Appel, 2011). Assuming that the way of life of modern agropastoralists resembled the way of life of ancestral ones, we can also argue that these societies were characterized by strong parental influence over mating, especially over daughters, with fathers dominating the marriage arrangements. This prediction is corroborated by historical records that indicate that arranged marriage was the typical form of mating in these societies (Apostolou, 2012). In one study, I compared the mating patterns of contemporary hunter and gathering societies with the mating patterns of contemporary agropastoral societies, and I found that arranged marriage was more prevalent in the latter (Apostolou, 2010). I also found that, in comparison to hunting and gathering societies, in agropastoral societies arranged marriage was more frequent for sons, while fathers dominated marriage arrangements more frequently than mothers. This evidence suggests that the agropastoral revolution strengthened parental influence, especially of fathers, on their male children.

Postindustrial Societies

Postindustrial societies, such as the United States, are technologically advanced and produce considerable wealth. Technology orientation requires a

prolonged time of training, which results in people delaying marriage and procreation in order to complete their studies and be able to participate effectively in the labor market. Furthermore, the produced wealth allows the creation of social protection systems, such as unemployment benefits and food coupons. Last but not least, individual rights are well protected by institutions such as the law and the police. These factors reduce considerably the opportunity cost of free mate choice, and consequently, the influence that parents exercise over their children's mate choices (Apostolou, 2017c). In particular, when they are to get married, children are financially independent from their parents, so the latter cannot use the former's financial dependence to impose their will. In addition, parents cannot employ physical force in order to do so as individual rights are well protected. Moreover, because children marry older, their parents are also older and, most likely, have ended their reproductive careers. In effect, the diverging opportunity cost of free mate choice decreases, as parents are not motivated to impose undesirable partners to their children in order to gain reproductive benefits for themselves (Apostolou, 2017c).

Even so, in the postindustrial context, there is still diverging opportunity cost. For instance, children could make mate choices that they consider good for themselves but could impair the social standing of their parents and their family in general, and could thus, compromise the fitness of their genetic relatives. There is also considerable converging opportunity cost, as children can make erroneous mate choices harming their own and their parents' fitness. In sum, in the postindustrial context there is an opportunity cost of free mate choice, which will motivate parents to reduce it. The prevailing conditions prevent parents form influencing mate choice directly, so they are likely to do so indirectly, predominantly by using psychological manipulation (for a more extensive discussion of psychological manipulation see Buss, 1987, 1992).

Sussman (1953) reported that parents employ means, such as "cajolery, persuasion, appeals to loyalty, and threats," in order to influence their children's mate choices. In a more recent study, I identified seventy-two acts of manipulation that parents use in order to influence mate choice (Apostolou, 2013a). The manipulation tactics fell into two broader categories, namely, twelve that parents use on their children and four that they use on their children's mates. Starting from the former, parents attempt to advise their children on who is the best mate for them, they closely guard their children to prevent them from engaging in undesirable relationships, they try to match their daughters and sons to desirable mates, they threaten their children with consequences if they continue an undesirable relationship, they try to bribe them out of an undesirable and into a desirable relationship, and they try to make them feel guilty that an

undesirable relationship harms the health of their parents. They also ask their children's friends or other family members to influence their children's mating behavior and also make comparisons between their children's mating behavior and the respective mating behavior of other individuals.

With respect to the tactic parents employ on prospective in-laws, they try to lure desirable mates for their children by promising them money and support, they invite them home for dinner and make them feel part of the family. On the other hand, they threaten undesirable mates with consequences if they do not terminate the relationship with their children, and they try to obtain information that could use against them. In one study, I asked people to indicate how likely these acts were to influence their behavior if the parents or their mates' parents employed them against them (Apostolou et al., 2015). I found that these acts were rated as moderately effective.

In the postindustrial context, parents are still more interested in controlling their daughters' than their sons' mating behavior (Perilloux et al., 2011). Nevertheless, mothers are more involved than fathers in influencing their children's mate choices (Apostolou, 2011). One possible reason is that, as opposed to the preindustrial, in the postindustrial context polygyny is not practiced and fathers cannot directly convert their children's mate choices in reproductive gain for themselves. In addition, individual rights are well protected, so fathers are constrained in using physical force on their children. In effect, the opportunity cost of free mate choice, and especially the diverging component, has decreased considerably for fathers who, as a consequence, are less motivated to influence their children's mate choices. On the other hand, the converging opportunity cost component remains relatively high, and due to paternal uncertainty, it is higher for mothers than for fathers (see above), which could explain the observed higher interest of mothers in influencing mate choice (Apostolou, 2017c).

Implications

Sexual selection refers to the selection forces that give rise to traits that enable individuals to gain access to members of the opposite sex (Andersson, 1994). Darwin (1871) identified two mechanisms of sexual selection, namely, intrasexual selection, or competition between members of the same sex for access to mates, and intersexual selection, where members of one sex choose members of the opposite sex. With respect to the latter force, it has been argued that females are usually the choosers, turning female choice into the primary force driving intersexual selection (Andersson, 1994; Darwin, 1871).

Nonetheless, the anthropological and historical evidence discussed above indicates that in ancestral human societies, female choice was a relatively weak sexual selection force, as women's mate decisions were largely controlled by their parents. A reduced capacity to exercise choice would translate into weaker selection: Traits that made a man more likely to be selected as a mate by women would offer to their owners limited reproductive benefits, because women's capacity to exercise choice was constrained by parental control.

On the other hand, a man's access to the opposite sex was largely determined by whether he would appeal to a woman's parents, especially her father, who was the primary decision maker in marriage arrangements. It follows that traits that would make a man more appealing as a son-in-law, especially to older men, would experience strong positive selection and will tend to increase in frequency in the male population. This being the case, parental choice, and especially male parental choice, has been one sexual selection force driving sexual selection (Apostolou, 2014). This force is unique in humans, as there has not been any other species recorded where parents control their children's mating behavior, choosing mates for them. Yet, such human uniqueness has not been recognized and incorporated into sexual selection models. In turn, scholars who employ evolutionary thinking in understanding human behavior adopt nonhuman animal models of sexual selection, which do not capture the way sexual selection works in our species. Sexual selection models need to be revised to incorporate parental choice as a sexual selection force and account for the patterns of mating found in contemporary and historical human societies. The revised models should subsequently be employed in understanding adaptations directing human mating behavior.

Moving on, one key insight that evolutionary psychology offers to the study of human behavior is that the human mind has been shaped in ancestral human societies which were different from our own. Accordingly, the mind and human behavior could be understood in reference to the selection forces operating in ancestral environments (Tooby & Cosmides, 2015). This insight could be employed in understanding phenomena the evolutionary origins of which look paradoxical in reference to contemporary environments. I will discuss next two such phenomena, namely, same-sex attraction and involuntary singlehood.

A considerable proportion of the population, estimated to range from 10 percent to 20 percent, experiences some degree of emotional and sexual attraction toward members of the same sex (LeVay, 2010). Same-sex attraction motivates people to divert part or the whole of their mating effort toward attracting mates of the same sex. As same-sex relationships do not lead to children, such attraction would face strong negative selection, which would

remove from the gene pool any alleles that predispose for it. Accordingly, same-sex attraction should be in very low prevalence in the population, which turns the relatively high observed prevalence of same-sex attraction an evolutionary paradox. This paradox could, to some degree, be resolved by taking into consideration the ancestral human condition. More specifically, in an ancestral context where mate choice was regulated, parents would match their children to opposite-sex partners irrespectively of their daughters' and sons' attractions. Accordingly, parental influence over mate choice effectively reduced the negative selection exercised on same-sex attractions, allowing such disposition to be in relatively high frequency in the population. The transition from a context where mate choice was regulated to a context where it is freely exercised took place very recently in evolutionary terms, so the prevalence of same-sex attractions observed in contemporary societies constitutes the result of these weak ancestral selection forces (Apostolou, 2016b).

With respect to involuntary singlehood, recent studies have found that almost one in two people experience poor performance in mating, meaning that they do poorly in starting and/or keeping an intimate relationship (Apostolou et al., 2019a; Apostolou et al., 2018). Such poor performance increases the likelihood of being involuntary single (i.e., to want to be in an intimate relationship but face difficulties in doing so). Studies find that almost half of people who are single are involuntarily so (Apostolou & Wang, 2019; Apostolou et al., 2019b). The most common reason people in Greece and in the United States give regarding why they are single is poor flirting skills; that is, people face difficulties in understanding clues of interest and in approaching prospective mates to initiate flirting (Apostolou, 2017d, 2019; Apostolou et al., 2020). Given the tremendous evolutionary importance of attracting mates, we would expect that selection forces would have endowed most individuals with a good flirting capacity so that the high prevalence of poor flirting capacity and the associated high incidence of involuntary singlehood constitute a paradox.

This paradox could be solved by taking into consideration that, during most of human evolutionary time, mating was controlled by parents who chose spouses for their children. Accordingly, individuals did not have to approach and flirt with prospective mates, so their flirting capacity was weakly associated with their mating success. It follows that selection forces were weak in forging flirting capacity, resulting in several people lacking good flirting skills. In a contemporary postindustrial context where people have to find mates on their own, this lack of flirting skills damages people's capacity to attract mate and results in higher incidence of involuntary singlehood (Apostolou, 2015b).

In conclusion, children's free mate choice is potentially costly for parents,

who are motivated to influence their daughters' and sons' mate choices in order to reduce the cost. Parental influence varies considerably across societies in strength, as well as in the way it is exercised. Parental influence has also important implications for understanding human mating behavior, which require considerably more research in order to be understood.

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CHAPTER 10

Beyond Sex: Reproductive Strategies as a Function of Local Sex Ratio Variation

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Abstract

Darwin was the first to offer an evolutionary explanation for widespread sex differences in mating strategies across animal taxa. However, initial applications of evolutionary approaches to the study of human behavior were met with resistance. In response, social scientists began systematically applying rigorous evaluations of evolutionarily informed hypotheses by way of testable predictions. Mate choice research was a key area for this early work, focused on demonstrating sex differences in mating behavior. Subsequent research has tempered some earlier conclusions, increasingly relating mating strategies to aspects of socioecology. In particular, the adult sex ratio has emerged as an essential demographic variable contributing to behavioral variability within and between the sexes, leading to frequency-dependent rethinking for the patterning of mating competition and parental investment. Empirical examination of the association between adult sex ratio and aggression, family formation, partnership stability, and risk-taking is a growing field of research cross-cutting various literatures. In this chapter, we first describe early theory motivating research on sex differentiated behavior, followed by recent frequency-dependent reexaminations of sexual selection. Second, we introduce the adult sex ratio as a central determinant of fitness payoffs to differing reproductive strategies. Third, we review empirical studies on the consequences of sex ratio variation, highlighting outcomes related to sociosexuality, family formation, and violence. Fourth, we detail the maturation of the field, and where theoretical and empirical work has unveiled complexities regarding reproductive strategies. Finally, we reflect on future directions, where

theoretical refinement is under way or needed, and highlight promising and novel research approaches.

Key Words: sex ratio, sexual selection, mate choice, sociosexuality, violence

Introduction

One hundred and fifty years following the publication of Darwin's foundational book on sexual selection (1871), evolutionary approaches to the study of human behavior are flourishing. Significant advances to evolutionary theory rapidly occurred during the 1960s and 1970s when insights from Charnov, Hamilton, Maynard Smith, Trivers, and Williams were integrated to provide a unifying theoretical framework relevant to the study of individuals and their behavior. During the late 1970s, social scientists began applying these theoretical developments from the rapidly emerging field of sociobiology to tackle questions on diverse topics from patterns of parental investment to warfare (Chagnon and Irons 1979). However, applications of evolutionary, approaches to the study of human behavior were not well-received initially (Laland and Brown 2011; Segerstråle 2000). Early (and continuing) criticisms of this approach included accusations of reductionism, genetic determinism, and slippery "Just So Stories" (sensu Rudyard Kipling) for the origins of particular traits and behaviors (Rose et al. 1984). In response, researchers began systematically applying rigorous evaluations of evolutionarily informed hypotheses by way of testable predictions (Blurton Jones 1984; Chagnon 1988; Hill et al. 1984; Winterhalder and Smith 1981). Consequently, while critics remain, evolutionary thinking has unequivocally enriched our understanding of human behavior.

Mate choice research was a crucible for the testing of evolutionary theory across the social sciences (Buss 1988; Symons 1979). This research focused on sex differences in the extent and nature of mating behavior, whereby differing patterns of parental investment and costs to reproduction were argued to produce distinct reproductive strategies for males and females (known as sex roles; Trivers 1972). Thirty years of subsequent investigation has tempered earlier conclusions, and research in the area draws on increasingly elaborate behavioral ecology theory that relates mating preferences to features of the social and natural environment (Pillsworth 2008; Schacht and Grote 2015; Scott et al. 2014). In particular, recent theoretical and empirical work has drawn attention to

facultative reproductive strategies in response to whether partners are abundant or scarce (Schacht and Borgerhoff Mulder 2015; Stone et al. 2007; Uggla and Mace 2017). Because individual reproductive options are structured by local partner availability, the adult sex ratio is an essential demographic variable contributing to behavioral variability within and between the sexes (Ancona et al. 2017; Schacht et al. 2017).

This recognition has led to frequency-dependent rethinking for the patterning of mating competition and parental investment within and among populations, as well as for the evolution of monogamy and social organization in our lineage (Coxworth et al. 2015; Kramer et al. 2017; Schacht and Bell 2016). In this chapter, we provide an overview of work performed by anthropologists, biologists, psychologists, and others who have examined the consequences of sex ratio variation for mating strategy diversity. In doing so, we consider reproductive behaviors broadly and draw on work from both small-scale and industrialized populations in which skewed sex ratios have differing origins and magnitudes.

Sex Roles

Darwin, who took it as a general observation that males were much more eager to mate than females, was the first to offer an evolutionary explanation for widespread sex differences in mating strategies. In his 1871 book, *The Descent of Man and Selection in Relation to Sex*, he proposed sexual selection as a mechanism to explain the evolution of competitive traits (e.g., elk antlers) and ornamentation (e.g., peacock tails) observed across animal taxa. He argued that these characters emerged not because of their benefit for survival (à la natural selection) but due to "the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction" (v. 1: 256). However, while his characterization of ardent males and coy females quickly became rooted in the evolutionary sciences, Darwin was unable to explain how these sex differences first emerged.

Following Darwin's insight, and motivated by a desire to evaluate the role of sexual selection on generating divergent sex roles, Angus Bateman tested the reproductive consequences among males and females for mating multiply (Bateman 1948). From his laboratory-based research on reproductive success among *Drosophila melanogaster*, he argued that "sexual selection is much more effective in males than in females" (363). Specifically because males experience greater variance in fertility (i.e., relatively more males fail to mate than females), sexual selection operates more intensely on males for characteristics that aid in

their ability to reproduce. Bateman reasoned that this outcome is rooted in anisogamy. That is, whereas females expend considerable energy in egg production, male reproductive success is not limited by sperm production but rather by access to mating partners. As a result, he argued that "there is competition between male gametes for the fertilization of female gametes" (363).

The role of initial asymmetries in gametic investment for explaining divergent sex roles was further advanced by Robert Trivers (1972) and his development of parental investment theory. Specifically, he argued that the sex that invests more in its offspring will be more selective when choosing a mate and "individuals of the sex investing less will compete among themselves to breed with members of the sex investing more" (56). Thus, the observation that males typically cared less was reasoned to result from their ability to compensate more rapidly than females, by producing new offspring if the current young died. That is, because males invest less initially as a consequence of anisogamy, they have a higher potential reproductive rate and benefit more from mating multiply than do females. Consequently, it was reasoned that selection would typically favor mate-seeking and competitive behavior in males and heavy investment in parental care in females.

In an extension of this model, Emlen and Oring (1977) incorporated variation in partner availability and predicted that as the number of available males relative to available females rises, so does antagonistic competition among males over the relatively fewer females. Under such intense sexual selection, males will be less likely to provide parental care after mating than females, creating positive feedback and selecting for greater investment in competition by males. These expectations overlap with an influential literature in the social sciences. It is well documented that men engage in more violent and risk-taking behavior than do women (Messner and Sampson 1991). Accordingly, it is expected that as the number of men relative to women increases, rates of family and social instability will increase as well (primarily due to the growing number of unattached, bachelor males; Hudson and den Boer 2002, 2004). Thus, there is a general expectation, across literatures, that a relative abundance of males will elevate levels of conflict (particularly between males over partners), reduce pair-bond stability, and decrease paternal investment.

Critique of the Standard Model

Where sex differences in reproductive costs are clear (e.g., pregnancy and lactation), expectations of divergent sex roles emerge from coherent logic

(Parker and Birkhead 2013) and empirical support (Janicke et al. 2016). Thus, tying premating asymmetries in investment to postmating patterns of care and competition has served as a useful "rule of thumb." For example, among mammals, male-only care is completely absent and females care alone in about 90 percent of species (Clutton-Brock 1991). However, how broadly applicable this "rule of thumb" is across animal taxa is increasingly being challenged. Across species, where parents provide postmating parental care, contributions of each sex varies considerably. Among birds, for example, 90 percent of species show biparental care (Cockburn 2006). Fish too challenge the typical characterization of sex roles; male-only care is nine times more common than female-only care across genera (Reynolds et al. 2002).

What explains this variation and divergence from the general "ardent male" and "coy female" characterization? As described above, an expectation from parental investment theory is that where males invest more in care, they will be less competitive (Trivers 1972). While this offers a description of a pattern of behavior, it does not explain what *motivates* males to care more, especially given their initially lower gametic investment (*contra* Bateman 1948). That is, why do pre- and postmating patterns of investment align for some taxa (e.g., mammals) and not others (e.g., birds)? While explaining differences in sex biases in parental care and competition will always involve taxonomic and historical contingencies (e.g., among fish, male parental care appears to result in fewer opportunity costs, i.e., lost matings; Hale and St Mary 2007; Reynolds and Jones 1999), models of sex role evolution must take into account the Fisher condition to be internally consistent (Houston and McNamara 2005, Kokko and Jennions 2008). Specifically, males cannot on average reproduce any faster than females if the adult sex ratio (ASR; ratio of males/females in a population) is even. That is, at the population level, when there are equal numbers of males and females, the reproductive rates of both males and females are the same. Accordingly, in spite of anisogamy, there is no inherent bias toward care by females if parents have identical future prospects of reproduction. On average they do, at least in populations with equal sex ratios (Kokko and Jennions 2003).

What then explains sex role divergence across animal taxa? As mentioned above, the ASR is an important consideration when calculating reproductive rates. If one sex becomes more or less common, the payoffs to care versus competition change. Specifically, the relatively rarer sex experiences greater costs to care given their elevated reproductive rates as a result of their scarcity (Kokko and Jennions 2008). Ultimately, while variability in mate quality (Wade and Shuster 2002) and paternity certainty (Houston and McNamara 2002) play important roles for the evolution of mating strategies, partner availability

fundamentally structures payoffs to investment in caring versus competitive behavior.

This insight is important not only for the evolution of sex roles but also for the patterning of individual behavior in response to real-time fluctuations in partner availability. Specifically, a key feature of this revised framework is its game-theoretical approach, which incorporates the relative scarcity of partners when modeling the sex-structured payoffs to reproductive behavior (Kokko and Jennions 2008; Schacht and Bell 2016). Put simply, a central claim of this approach is that, in general, the profitability for males to invest in mating effort increases when more, not fewer, mating opportunities are available. Males that pursue a mating-effort intensive strategy when mates are rare may find themselves spending longer periods of time in between reproductive events than if they were to stay with their initial partner and care or mate guard. Thus, when males are in abundance and surrounded by competitors, revised models expect them to reduce, not increase, mating effort.

Empirical examination of the association between ASR and aggression, family formation, partnership stability, and risk-taking is a growing field of research cross-cutting various literatures. Drawing on research from anthropology, biology, sociology, psychology, criminology, and related disciplines, we evaluate current understandings of how various behaviors that can be interpreted as mating effort vary with the sex ratio. Despite common expectations of male excess leading to increasingly negative outcomes, empirical support often points in the other direction in line with critiques of the standard model of sexual selection and parental investment theory. In the following section we review findings broadly, targeting behaviors both hypothesized and shown to be sensitive to sex ratio variation.

Sex Ratio as a Field of Study

While the role of the ASR on mating behavior across human and nonhuman animals has been recognized since at least the nineteenth century, it remained largely unincorporated into active research until the early 2000s. It was Darwin (1871) who initially noted the relevance of ASR variation for sexual selection in his chapter “Numerical proportion of the two sexes.” Darwin’s key insight was a realization that competition for mates could relate to their relative abundance.

Around this time period, sociologists too noted the importance of ASR for relationships. Beginning with seminal work by Dubois (1899) highlighting the role of partner availability on pair-bond stability, and later, with research by Groves and Ogburn (1928) on marriage patterns, relationship formation was

argued to follow principles of an economic market. Not only was the proportion of members of the opposite sex associated with rates of marriage, partner availability was also shown to influence the importance of particular traits in a mate. Independent of this work in the social sciences, evolutionary biologist Ernst Mayr (1939) highlighted extreme ASR variation across various bird species, arguing that sex ratios and mating systems were related. He noted that monogamy was generally more common under male-biased ASRs and polygyny under female-biased ASRs. Nonetheless, after decades of research, and despite partner availability being a fundamental demographic characteristic affecting mating options across populations, the role of the ASR for reproductive strategies remained understudied until relatively recently (Kokko and Jennions 2008).

Increasingly, however, research across the biological and social sciences demonstrates the role of partner availability on reproductive strategies, both within and across species. For example, behavioral ecology work in soapberry bugs *(Jadera haematoloma*) finds male behavior to respond facultatively to female availability (Carroll and Corneli 1995). Specifically, when males are in excess and females are in demand, males engage in mate-guarding behavior. However, when potential partners are plentiful, males target short-term mateships with multiple females by way of intrasexual competition. Similar findings have emerged from the bird literature as well. For example, in bird species with male-biased ASRs, male paternal care (and even polyandry) predominates (Liker et al. 2014). Ultimately, results from this work demonstrate an emerging pattern between local sex ratios and mating systems across animal taxa. That is, generally, monogamy is found to be associated with male-biased sex ratios and low variance in male reproductive success, whereas, polygyny is associated with female-biased sex ratios and high variance in male reproductive success (Kokko and Jennions 2008).

The results from the nonhuman animal literature are consistent with research from the social sciences targeting a frequency-dependent approach to behavior (Becker 1981; Guttentag and Secord 1983). Mating market theory, as a guiding framework, centers on the general expectation that when men are rare, they will behave more promiscuously, offering little parental investment while still being able to obtain partners. However, when women are in short supply, men will be more willing to commit to a single partner and, depending on the culture under study, adopt behaviors consistent with women's relationship preferences. Ultimately, according to both behavioral ecology and mating market approaches, mating behavior is seen as a response to sex-structured payoffs to partner availability. In the next three subsections, we review results targeting three

emerging categories of findings among sex ratio studies of behavior—sociosexuality, marriage and family formation, and aggression and violence.

Sociosexuality

As introduced above, mating market theory eschews simple sex-based arguments and instead focuses on variable response to context (Guttentag and Secord 1983). Likewise, recent reformulations within sexual selection theory reconsider predictions drawn from sex differences in optimal mating rates and costs to reproduction (Kokko and Jennions 2008) and emphasize that reproductive strategies are facultative responses to partner availability. The number of males and females in a population can be thought of as a mating market, which operates by supply-and-demand economics. The rarer sex has more bargaining power and can leverage their scarcity to realize their preferred mating strategy, while the more common sex caters to the preferences of the rarer sex in order to acquire a mate (Becker 1981; Guttentag and Secord 1983).

Accordingly, mating behavior is predicted to be responsive to sex-structured payoffs to partner availability (Kokko and Jennions 2008). One measure of investment in mating effort is the sociosexual orientation inventory (SOI; Simpson and Gangestad 1991). Sociosexuality scores are used to evaluate an individual's willingness to engage in uncommitted sexual activity. Individuals who score high on the SOI scale (termed "unrestricted") display a reproductive strategy of multiple short-term, uncommitted sexual relationships while those scoring low on the SOI scale ("restricted") prefer longer-term, committed relationships. In a survey administered across forty-eight countries, sociosexual orientation was negatively associated with the national sex ratio (Schmitt 2005). That is, while sex differences in willingness to engage in uncommitted sex were observed across countries, both men and women were more restricted where women were rare than where women were abundant. Follow-up work targeting community rather than country-level sex ratios corroborates mating effort flexibility; however, at male-biased sex ratios, willingness of men and women to engage in uncommitted sex was indistinguishable. Specifically, men's sociosexuality was unrestricted when partners were abundant; however, when men were in excess, both men and women were equally restricted, a result challenging some persistent views on sex differences in sexual behavior (Schacht and Borgerhoff Mulder 2015).

Another line of evidence regarding mating effort comes from research on sexually transmitted infections (STIs). Here studies from the realm of public health have helped unite two separate areas: sex ratio skew among some ethnic

groups in the U.S. (e.g., non-Hispanic African American) and the higher vulnerability to HIV/AIDS among these groups. In the US, more than 90 percent of whites live in areas with balanced sex ratios; whereas, more than 90 percent of African Americans live in female-biased areas (Adimora et al. 2013). Tough-on-crime policies, in particular, have contributed to these persistent male shortages across African American communities. Ultimately, high incarceration rates of men generate female-biased sex ratios and are associated with higher rates of sexual concurrence—a significant risk factor for HIV infection (Pouget et al. 2010). However, this outcome is not unique to female-biased sex ratios but appears to be a response broadly shared across cultures where men are limited in their ability to provide resources and/or it takes the investment of more than one man to meet household resource needs (Beckerman et al. 1998).

The above pattern of higher concurrency and unrestricted sociosexualities in female-biased ASRs is consistent with mating market predictions. However, the association between risky sexual behavior and the ASR is mixed (see Bien et al 2013). Studies from the United States, China, and India report that while men are more likely to delay sexual debut when females are scarce, they are more likely to purchase sex (Senn et al. 2010; South and Trent 2010; Trent and South 2012). Thus, "more men" may lead to a higher risk of HIV/STI infection not due to sexual concurrency (both men and women have fewer sexual partners in male-biased areas; Smith and Subramanian 2006) but due to higher engagement in transactional sex after debut.

Marriage and Family Formation

The role of sex ratio variation in marriage, family formation, fertility, and timing of childbearing is an additional area that has been researched extensively across the social sciences (Fossett and Kiecolt 1991; Guttentag and Secord 1983; Pedersen 1991). Data on childbearing and family formation are usually widely available and can be compared across cultures, allowing for an array of different measures of pair-bond commitment to be tested. Prominent concerns are that relatively more men in a population will lead to pernicious outcomes regarding violence and brittle family ties (Hudson and den Boer 2002, 2004; Messner and Sampson 1991). However, studies have demonstrated that where men outnumber women, behaviors that promote family formation and stability are more common (Albrecht et al. 1997; Schacht and Kramer 2016; Trovato 1988). Men are more likely to marry (Guttentag and Secord 1983, Schacht and Kramer 2016), marriages last longer (Otterbein 1965; South and Lloyd 1995; South et al. 2001; but see Obersneider et al. 2019), and fertility is higher (Schmitt and Rohde 2013;

South 1988) in male-biased areas.

Greater male investment in relationships and parenting effort may explain these patterns (Pedersen 1991). However, this facultative aspect of male behavior has received much less attention than mating effort expressed as violence (see below). Nonetheless, this perspective also offers insights into fragile family outcomes in areas with more women. For example, female-headed households and out-of-wedlock births tend to be higher in female-biased contexts (Barber 2001; Schacht and Kramer 2016) and are coupled with lower rates of contraceptive use (Lippa 2009). A mating market perspective on family formation suggests that when men are scarce, women might need to be more sexually permissive in order to secure a mate (even if just for the short term). In such contexts, men have relatively more partner options than women and women's ability to be demanding in their choice of mate, or in their expectations of commitment, is limited. Behavioral ecology work among nonhuman animals supports a similar pattern. In bird species, both pair-bond stability and infidelity vary in tandem with the adult sex ratio, with higher rates of pair-bond dissolution and promiscuity when females outnumber males (Liker et al. 2014).

While outcomes related to family formation and reproduction seem to show a coherent picture, our own separate work in this area has generated findings that diverge. Schacht and Smith (2017), using nineteenth-century data from the US state of Utah, found that women were more likely to give birth at younger ages in *male*-biased districts. Conversely, Uggla and Mace (2016), using data from Northern Ireland from the early 2000s, found that entry into motherhood was earlier in *female*-biased areas. Both of these analyses used individual-level data, small districts for the local sex ratio, and longitudinal designs for testing the timing of first birth, yet they still produced opposite outcomes. One insight to draw from these diverging results is to pay attention to the particular sociocultural context, or the "culturally mediated mating arena" (Schacht and Smith 2017). In nineteenth-century Utah, reproduction was confined to marriage, and thus earlier childbearing signifies earlier male commitment to a stable pair-bond. In contemporary Northern Ireland, however, later ages at childbearing are associated with more stable relationships and lower rates of single parenthood. Thus, both earlier and later entry into parenthood can be interpreted as greater commitment to a relationship, depending on the context under study.

Aggression and Violence

A slightly male-biased sex ratio at birth is characteristic of many nonhuman and human populations (James 1987), yet sex ratios often become quite skewed

in adulthood (e.g., excess male mortality or sex-biased migration; Das Gupta et al. 2009). For example, large parts of China are projected to have a 15–20 percent excess of young men over the next several decades as a consequence of son preference and female-biased abortion and infanticide (Hesketh and Min 2012). Because being male is one of the best individual-level correlates of violence (Messner and Sampson 1991), these statistics have raised considerable alarm (Hudson and Den Boer 2002, 2004). An increased number of unmarried men resulting from the male-biased sex ratio is a concern because these unattached, risk-prone men tend to engage in more antisocial and violent behavior than married men (Sampson et al. 2006). Moreover, with partner rarity, males are argued to face elevated levels of competition to secure a mate, potentially leading to greater violent interactions between males (Messner and Sampson 1991).

On the other hand, researchers employing a mating market approach to male violence have argued the opposite. When males are in abundance and surrounded by competitors they are expected to reduce, not increase, mating effort. This is because payoffs to short-term mating orientations and agonistic male–male competition can be better realized when potential partners are available (as they are in female-biased sex ratios). A key consideration is that the intensity of sexual selection (as gauged by male variance in reproductive success) is sensitive to partner availability. Specifically, both human and nonhuman animal research has indicated elevated male reproductive skew where females are in excess (Schacht and Borgerhoff Mulder 2014; Szkeley et al. 2014). This would seem to indicate that violent male competition will be more common at female-biased sex ratios.

Studies evaluating these competing expectations, however, find that biased sex ratios (in either direction) are inconsistently associated with elevated rates of crime and violence (Messner and Sampson 1991; Schacht et al. 2014; Uggla and Mace 2015). Rates of violent crime, homicide, sexual assault, and property crime have all been found to be both positively and negatively associated with the sex ratio (Barber 2000; Drèze and Khera 2000; Edlund et al. 2013; Filser et al. 2021; O'Brien 1991; Schacht et al. 2014; Trent and South 2012). Why might this be the case? Notwithstanding the wide variation in the nature and quality of the violence measures used, because there is a wide variety of forms that mate acquisition strategies can take, it is inaccurate to assume that mating competition will necessarily involve violent behavior. For example, although a minority of men might try to improve their prospects on the mating market through violent means, if the majority of men typically pursue other strategies to acquire a mate (e.g., economic status acquisition or cues of commitment; Kaplan and Lancaster

2002), violence is unlikely to show a significant association with the ASR. In addition, the causes of violent behavior can be unrelated to mating competition and causally linked to substance abuse, economic inequality, or gender role socialization.

Ultimately, despite vocal arguments regarding men's violence toward potential competitors on the partner market, evidence remains mixed in terms of male intrasexual competition in response to ASR. An uncritical acceptance of the "more males, more violence" prediction from traditional theory is unwarranted; there is no straightforward pattern of violence in relation to sex ratio in the literature. Although simple stories are often sought, this varied relation between violent crime and sex ratio is unsurprising. Modern sexual selection theory identifies diverse factors influencing male strategies that complicate predictions about the effects of ASR on either mating competition or violent behavior. Key factors such as the degree of intrasexual variation in mate quality (Queller 1997), variability in payoffs to agonistic competition (Arnold 1994), and the nature and extent of female choice can dramatically influence whether the optimal male mating strategy should include violence. Moreover, mating and parental effort are not necessarily mutually exclusive and paternal investment can sometimes entail violence (as in some forms of property crime). Clearly, we have considerably more thinking to do when attempting to use sexual selection to understand patterns of violence in humans. Below we outline a series of considerations that could help to shed light on not only ASR and violence but reproductive strategies more generally.

A Maturing Field of Study

Despite a growing body of work over the past several decades, summarizing the current state of the sex ratio literature is a challenging endeavor. At the core are debates on fundamental questions of sexual selection and foundational theory therein: will partner scarcity increase mating effort (as per traditional models; Emlen and Oring 1977; Trivers 1972) or decrease it (as per the reformulated perspective). But applying a sex ratio "rethinking" to reproductive strategies does not rely on a simple retooling from "more males = more violence" to "more males = less violence". Instead, empirical research and theoretical reformulations of sexual selection theory point to nuanced and place-based predictions (Kokko and Jennions 2008; Schacht et al. 2014). In other words, it is clearly inappropriate to assume an ASR association (one way or another) without consideration of other factors that simultaneously impact mating strategies. Accordingly, in Box 10.1 we detail important methodological

considerations as well factors such as individual variation, root causes of sex ratio bias, and cultural norms that all impact the patterning of reproductive strategies in addition to, or in concert with, ASR variation.

One focal reason that it is difficult to get a coherent picture of the literature to date is that sex ratio measurements vary widely across studies (see Box 10.1). Researchers variably consider all adults (or some limited age category of adults), only adults who are single, the entire population (inclusive of sexually immature individuals), or partner markets separated by ethnic group or migrant origin (Angrist 2002). However, although a one-size-fits-all measure would make comparative work more straightforward, cross-cultural research on the topic has highlighted that entry and exit from the mating market is highly variable across place (e.g., Low et al. 2008; Walker et al. 2006), requiring place-based variation to be considered in our methodological approaches. For example, in some locales, males may either be removed from the mating market at marriage (some strictly monogamous societies) or remain active participants until near the end of their life (some polygynous societies). Moreover, the unit of analysis is highly variable across studies—from national- to zip code-level sex ratio measurements. Studies where both the ASR and the outcome in question are aggregated (e.g., national-level data) run the risk of suffering from the ecological fallacy, whereby the relationship at the area level does not necessarily translate to individual-level behavior (Pollet et al. 2017). In fact, a recent paper on the relationship between sex ratios and crime shows a negative (nonsignificant) association at the municipality level but a positive association when individual controls are incorporated (Filser et al. 2021). Obviously, the bookends that we place on our sex ratio variables, as well as the level of population aggregation, will themselves affect associations with variables of interest. Accordingly, work targeting mating effort responses to sex ratio variation should attempt to examine locally relevant mating pools (e.g., those geographic areas in which individuals live and work) as well as sex ratios measures that include those in the mating market (i.e., when do men and women age in and out?).

Recently there has also been increased attention on the processes that generate uneven sex ratios. This is crucial because ignoring the causes of sex ratio skew can result in failure to appropriately predict mating strategy variation. For example, many female-biased ASRs in urban areas are the result of female migration for higher education and employment opportunities (Rauhut and Littke 2016). Given that women who move to pursue tertiary education are less likely to commence childbearing at younger ages, it is erroneous to conclude that lower fertility rates in female-biased areas are invariably due to lesser male relationship commitment. In another migration-related example, many young

men migrate to the US state of Alaska for short-term labor opportunities (Garcia and De Castro 2017). If temporary immigration self-selects for men who are not seeking committed relationships, they may pursue mating strategies that differ from men in other male-biased populations. Moreover, the labor opportunities that are the cause of migration, such as mining and construction, are frequently dangerous in themselves, an issue that might further select for men who are risk-prone. Thus, male-biased populations comprised of short-term resident males might experience higher rates of male aggression and lower rates of family stability than male-biased populations comprised of long-term residents. In other words, considering the variation across and distribution of individuals in terms of their psychological characteristics, such as degree of future discounting or risk-taking propensity, is necessary to understand the consequences of their movements.

Box 10.1. Six Reasons the Adult Sex Ratio Is Measured Differently across Studies

Conceptually, the adult sex ratio is a straightforward demographic characteristic that is widely available for populations cross-culturally. This, potentially, allows for comparative study within and across societies, as well as between human and nonhuman animals. Yet, the sex ratio literature is fraught with dissimilarity in how to operationalize the ASR. Given the many possible ways to quantify the relative number of men to women in a society, what are the best practices? Here we list six considerations that may help to both explain some inconsistencies in results across studies and assist in future research.

1. Who is available? The once central concept from biology of the operational sex ratio—the ratio of males to females ready to mate (Emlen and Oring 1977)—is for the most part overshadowed by measures of the adult sex ratio (all men:women in a population). The preference for using the adult sex ratio is for both theoretical as well as practical reasons. For example, operational sex ratio calculations involve removing women who are pregnant. This practice is problematic because female pregnancy status is often unknown, and removing these women arises from the, likely inappropriate, assumption that they are no longer active participants in the mating market.
2. Which ages? The age range used when constructing a sex ratio should match the research question. Often researchers apply some range to reflect reproductive-aged individuals (e.g., fifteen to fifty for both sexes), but narrower or broader age ranges might be warranted depending on context, outcomes of interest, and data availability. While rare, future work might benefit from employing age ranges that are variable and tied to an individual's age (e.g., their mating pool is opposite sex members -5/+10 years to their own for women and vice versa for men; see, e.g., Lyngstad 2011).
3. Definition of the mating pool (1)? The sex ratio is by necessity an aggregated variable and there are differences in the level of aggregation, and by extension the implied mating market, from countries, or large states or provinces, to the village level. Larger units of aggregation are likely

particularly problematic because they do not reflect locally relevant ratios of available partners to competitors for an individual.

4. Definition of the mating pool (2)? In most empirical studies based on census data, the sex ratio is derived from some residential area. However, groupings that constitute the mating market are unlikely to be bound simply by a governmental reporting district. Instead, they are likely to include, for example, those from a shared ethnic group for example, those from a shared ethnic group (Angrist 2002) or other contexts (e.g., such as workplaces or occupational domains; Svarer 2007, Uggla and Andersson 2018).
5. When does ASR matter? The timing of the exposure to mate scarcity or surplus is another important factor. That is, are individuals sensitive to dynamic trends in sex ratio variation, or are responses largely shaped by partner availability at some early time period (e.g., sexual debut). Longitudinal designs are rare, and most often the current ASR is used to predict behavior or attitudes as opposed to sex ratio during development (but see Schacht and Smith 2017).
6. How to count: a ratio or a proportion? The ratio-based expression of ASR is problematic because it is bounded by zero at one end and unbounded at the other end (i.e., positive infinity). Thus, the ratio is asymmetric around 1.0, and the same extent of male versus female bias leads to a very different scaling toward zero or toward positive infinity (Ancona et al. 2017). For this reason, researchers are increasingly turning to ASR as calculated as a proportion ($N_{\text{males}}/(N_{\text{males}} + N_{\text{females}})$) to avoid possible issues related to statistical interpretability.

An implicit assumption of much ASR work is that all individuals will be affected by mate availability equally. This assumption is inappropriate given the role of individual heterogeneity in mate quality and mating behavior. There is often more than one way to pursue or retain a mate (e.g., signal a willingness to invest or mate guard) and the choice of strategy depends on, for example, an individual's mate value (e.g., Daly and Wilson 1982; Uggla and Mace 2015). This is analogous to considering behavioral variability as reaction norms that vary by phenotypic and environmental variation. Whether an individual who seeks a partner, for example, opts for embodied capital accumulation versus mate-poaching, will depend on many factors, such as their access to employment opportunities, physical prowess, and attractiveness or the severity of sanctions on criminal behavior, if detected. Research targeting aspects of individual heterogeneity on reproductive strategies increasingly incorporate socioeconomic measures into studies of sex ratio variation. For example, birthrates have been shown to vary by ward-level measures of wealth and ASR in England (Chipman and Morrison 2013). Specifically, female-biased sex ratios are associated with higher birthrates at younger ages in poorer areas but not in richer areas. Similar work based on historical US data finds that as the ASR becomes more male-biased, the effect of a man's socioeconomic status on his ability to marry becomes stronger, possibly indicating that women put higher demands on prospective mates when mates are plentiful (Pollet and Nettle 2008). Other work targeting education levels, finds that in male-biased wards in Northern Ireland,

women's level of education was not associated with likelihood of cohabitation, but in female-biased areas women with higher education were more likely to be partnered (Uggla and Mace 2017). One conclusion is that it is only when women are plentiful that their relative status matters for being in a long-term pair-bond. If we assume that ASR will affect all individuals of a sex equally, we ignore the fact that highly desired partners will presumably be less (negatively) affected by the relative surplus of competitors. Going forward, it would likely be fruitful to explore such heterogeneity over a broader range of individual traits linked to mate value.

Finally, cultural norms have powerful effects on variability in behavior across societies. When applying evolutionary models, researchers regularly predict mating strategies to be responsive to the costs and benefits imposed by the local ecology. However, these trade-offs are not uniform across place and the freedom individuals have to engage in a particular behavior depends on local constraints (e.g., in the form of societal structures or cultural norms; Borgerhoff Mulder and Schacht 2012) that complicate universal interpretations of mating behavior under skewed sex ratios. For example, males with lower chances of securing a partner may be particularly risk-prone and aggressive regardless of ASR. Such circumstances arise when sociocultural systems exclude sectors of the male population from mating. In India, for example, the caste system and hypergyny create a pool of males with virtually no opportunities for marriage. Indian regions with male-biased ASRs and the highest rates of homicide overlap with those that most rigorously enforce the caste system (Dreze and Khera 2000; Mayer et al. 2008), which means that purported claims for the association between ASRs and violence in India need some unpacking. Conversely, we can consider the impact of ASR in societies with liberal family patterns where premarital cohabitation is the norm and relationship dissolution occurs, largely without social stigma, as in the Nordic countries (Sandström and Garðarsdóttir 2018). The combination of a strong welfare state and high gender equality means that individuals (regardless of gender or economic status) are legally and practically able to dissolve a union, and it is common to keep sharing childcare responsibilities after separation (Cooke et al. 2013; Duvander and Korsell 2020). Accordingly, in contexts such as these, the ASR is likely to have a different impact on patterns of marriage and separation than in places where women and men adhere to traditional family norms, marriages are maintained for instrumental and/or religious reasons, and women are more financially dependent on men.

Future Work and Applied Directions

The very traits that make surveys so efficient for data collection among, for example, US samples, are challenges that impede cross-cultural comparisons, especially between the industrialized West (WEIRD societies: Western, educated, industrialized, rich, and democratic; Henrich et al. 2010) and industrializing or non-industrialized (non-WEIRD) societies. Experimental survey techniques excel in maximizing study sample sizes per unit time, and surveys can be administered relatively simply with minimal time investment due to subjects' education levels and experience with survey methods. However, concepts regarding mating and reproduction do not necessarily translate neatly across societies, requiring time-intensive ethnographic work to provide a fuller view of behavioral motivations and constraints. For example, researchers often turn to the SOI (as described above) to evaluate sociosexuality. One question on the SOI asks the subject to respond to the statement, "sex without love is OK," on a scale from 1 to 9, strongly disagree to agree. While among Western samples, where romantic love between sexually committed partners is idealized, those who strongly agree with the statement are indicating an unrestricted sexual preference. However, across many societies love does not usually precede sex and marriage. Instead, a common global practice is for parents to arrange marriages, as romantic love does not enter into the inception of the union; rather, the desire is to tie two sets of families together, socially and economically. Thus, how to appropriately characterize sociosexuality (as restricted vs. unrestricted) will be heavily context dependent. A detailed insight from the population under study, and nuanced aspects of its particular sociocultural milieu, enables a fuller view of the mating market and its structural components, along with the norms that guide strategy diversity. Thus, more data amassed across non-WEIRD populations are necessary to better understand the patterns of human mating effort. Although such endeavors are time-consuming and costly, they facilitate comparing both similar and different outcomes and provide a comprehensive picture of how family formation, relationship commitment, and competition occur across societies.

Moreover, much of the literature here focuses on how the sex ratio where individuals live (defined in various ways, see Box 10.1) is linked to mating behaviors. Of course, this begs the question: how can we be certain that this aggregate statistic accurately reflects how individuals perceive their odds in the mating market? Given that natural experiments are extremely rare (see, e.g., Grosjean and Khattar 2019 for a quasi-experimental approach), and randomized controlled trials not feasible, studies that use priming methods (e.g., vignettes

featuring scenarios with many or few mates, or showing an unequal number of photos of same and opposite sex individuals) can complement observational studies. Recent experimental work, where individuals were allocated to different groups and then asked about preferred mating behaviors, reported differences between experimental and control conditions. For example, manipulated sex ratios have been found associated in predictable ways with the timing of family formation versus career activities (Durante et al. 2012), preferences for facial cues indicative of mate quality (Watkins et al. 2012), and hypothetical measures of jealousy and mate-guarding tendencies (Arnocky et al. 2014).

This work opens up an additional line of inquiry exploring whether objective and subjective measures of mate availability align. That is, are individuals' perceptions of mate availability accurate for the area in which they live? Efforts of this kind are rare, but studies thus far have found that there is little consistency between the objective statistics of the relative number of men to women (ASR) in an area and the perceived mate availability (Filser and Preetz 2021; Gilbert et al. 2016). However, subjective measures of sex ratio in Germany have been found to predict family formation for both men and women, suggesting that the subjective measure and its determinants need to be further assessed (Filser and Preetz, 2021). This work raises additional questions about how well a researcher's objective measure of a sex ratio appropriately reflects an individual's mating market. That is, an individually relevant ASR measure may not be bound by a particular geographic area but instead may be tied to an occupation or a narrower (or even more diffuse) social network. For example, future experimental research could be targeted to individuals who work in professions or are enrolled in fields of study in which one sex is overrepresented in everyday life (e.g., military personnel or anthropology undergraduates). Although there are obvious issues of self-selection in such groups, if appropriately considered, they might aid our understanding of which sex ratio matters to the individual.

In addition to expanding the type of data and populations commonly under study, future insights may come from considering a broader range of outcomes. Incorporating alternative and more fine-grained measures such as relationship satisfaction and bargaining over household tasks could aid in our understanding of dynamics that are not captured by divorce, separation, or fertility. Furthermore, although much emphasis has been placed on relationship patterning, mate quality has received little attention from a mate availability framework (but see Schacht and Grote 2015). This is surprising because when faced with mate scarcity, available options include delaying reproduction, changing mate criteria, and moving to another place. Whereas migration has

often been incorporated as a cause for sex ratio skew, it is rarely explored as a consequence. If the partner market is not promising where one is, individuals may have the opportunity to try their luck elsewhere. Moreover, compared to the large interest in the covariation between violence and male abundance, there is very little knowledge of how parenting effort varies with ASR. Because of the facultative nature of paternal investment in humans, it would be valuable to explore male care as a function of local partner skew across contexts. Finally, a point that we detail in Box 10.2 is that female competition is understudied—both generally in terms of reproductive strategies and specifically in terms of sensitivity to ASR variation.

Finally, the study of sex ratio skew has several policy implications, as well as the potential to unite several areas of broad public health significance. Although research outcomes range from the relatively benign to the life threatening (e.g., teen pregnancies, divorce rates, and intimate partner violence), the potential health consequences of the risky behaviors of many mating strategies are phenomena that preoccupy social scientists, population health scholars, and policymakers. For example, rising rates of depression and suicide are of concern for the many men who have slim prospects of finding a female partner due to the extreme male surplus in many regions of China (Zhou et al. 2013). Moreover, public health findings on risky sexual behaviors and STIs is an area of clear patterning with sex ratio skew. Thus, an important message is that imbalanced sex ratios lead to several harmful outcomes that are interlinked. Individuals who might under typical circumstances already face higher disease risk, lower family stability, loneliness, and more turbulent life experiences, may see these outcomes worsened when incentives for competition are higher.

Conclusion

Sex ratio research has advanced substantially since Darwin's initial considerations of the "numerical proportions of the two sexes" one hundred fifty years ago. While ignored for much of the twentieth century, recent frequency-dependent questioning of traditional perspectives on sex differences has helped reveal the rich tapestry of factors motivating reproductive strategies. Through a consideration of partner availability, patterns of behavior ranging from male commitment to female promiscuity become predictable. Empirical and theoretical insights have come from many disciplines across the social and biological sciences, each contributing their methods and disciplinary lens, yet many questions remain on how ASR affects mating strategies.

Some consequences of sex ratio skew present a more uniform empirical

picture than others. For example, while family formation outcomes show clear patterns, theoretical as well as methodological issues leave us without a simple story of male excess leading to more or less violence. Regardless, a key take-home point is that even where results appear coherent, outstanding questions remain (or appear) that should be tackled through an awareness of local cultural norms, an understanding of the influence of individual heterogeneity on strategy adoption, and an assessment of how the partner market is operationalized and perceived within a particular context. And, crucially, the effects of ASR may be intimately tied to the root causes of imbalance (e.g., economic migration); therefore, this relationship needs careful consideration.

Despite the important methodological and theoretical challenges remaining, we note a resounding applied value for ASR research on physical, sexual, and mental health well-being of men, women, and families. While these matters of universal concern will not be alleviated altogether by ASR scholars, insights to date are promising and strongly attest to the impact of mating scarcity and surplus on persistent and thorny societal challenges. Ultimately, we look forward to an expanded consideration of populations under study, and to more ethnographic data, to help fill in the gaps for our understanding of variation in reproductive strategies—beyond sex.

Box 10.2. Female–Female Aggression

> "Most … naturalists … admit that the weapons of male animals are the result of sexual selection. But many naturalists doubt, or deny, that female animals exert any choice."
> (Darwin 1882: Barrett 1977, p. 278).

This statement by Darwin was no exaggeration regarding scientific approaches to the study of evolution during the nineteenth century. For example, Alfred Wallace (the co-originator of Natural Selection) argued that female choice had little to no importance in evolution (Cronin 1991; Wallace 1889). This view (accepting the role of male competition but rejecting female choice for sexual selection) came to dominate evolutionary biology for the first half of the twentieth century. And, not only did scientists doubt that females had the capacity to be discerning, they also opposed claims that females engaged in reproductive competition over partners. These views were rooted both in empirical observation - male traits (e.g., the peacock's tail) and behaviors (e.g., male takeovers among lions) were (are) typically more conspicuous - and cultural norms in the US and Europe at the time. Behavior and morphology were approached through a patriarchal lens, and Victorian

views related to human sexual divisions affected scientists' interpretations of behavior (Cronin 1991).

This bias has persisted, with much of the sexual selection literature focused on male rather than female reproductive strategies (Hrdy 1986). This tendency exists in the sex ratio literature as well, despite increasing recognition that females respond facultatively to partner availability, and that they too can benefit from increasing mating effort (Brown et al. 2009; Hrdy 2000). For example, violent behaviors have regularly been shown to be more common among single women (e.g., Campbell et al. 1998), as they are for men (Sampson et al. 2006), possibly signaling that those in the mating market are more likely to engage in violent mating effort. However, there is little support for the claim that women's violent behavior correlates with the local sex ratio (Campbell et al. 1998; Swartz 2006). Why might this be the case; is female mating effort unassociated with partner availability? We argue that this conclusion is premature. For example, research on female–female violence using same-sex criminal behaviors has been explored with homicide data. These data are problematic because female–female homicides are extremely rare and, as such, data of this kind may be too coarse to detect whether there is indeed violent competition among women. Moreover, when generating predictions, it may be inappropriate to assume that female strategies, in response to partner availability, simply mirror male strategies given sex differences structuring reproductive payoffs to a particular behavior.

Accordingly, an additional consideration is that women may be more likely than men to compete through less conspicuous (and thus harder to detect) nonviolent means, such as verbal and/or indirect aggression (e.g., vocalized threats and social exclusion). This has led researchers to examine other forms of aggression as possibly more relevant outcomes of study for female competition (Björkqvist 1994). As with violence, single women are more likely to engage in or report employing indirect aggression than married women, giving some indication that indirect aggression is invoked in female mating competition (Stone 2015). However, again, results from the few studies of indirect aggression (gossip, nonviolent competition) as a function of the ASR are mixed: some report a negative effect (Arnocky et al 2014) while others find no association (Stone 2015). As we argued above, any conclusions would be premature given the limited research in the area, and the glaring lack of study of female competitive strategies (compared to the ink spilled on males) in the literature generally. Thus, future work targeting alternative female strategies in response to partner competition (e.g., labor market effort and physical attractiveness) could yield valuable, and much needed, insight into the forms

that female intrasexual competition may be taking.

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CHAPTER
11

Mating Strategies in Sexually Egalitarian Cultures

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Abstract

Cross-cultural empirical research testing evolutionary perspectives and human universals are important. There is considerable variation in women's rights, traditional gender roles, and political influence across different societies. Competing theories provide different explanations and predictions for sex differences observed in humans. Social role theory explicitly predicts a reduction in sex differences in more gender egalitarian societies due to societal influence on gender roles, whereas sexual strategies theory, although not being dismissive of cultural influence or effects of local ecological factors, predicts more stable sex differences based on parental investment theory and women and men have faced different adaptive problems throughout evolutionary history. Here we present more than a decade of empirical research from Norway, one of the most egalitarian societies in the world. We find no support for consistently smaller sex differences in samples from Norway in interest in sexual variation, sociosexuality, partner preferences, reasons for sex, sexual initiative and response, sexual over- and underperception, sexual regret and postcoital emotions, jealousy responses, or derogation and self-promotion. We conclude from these many studies that empirical predictions from social role theory are not supported. In contrast, the strong pervasiveness of sex differences across sexually egalitarian cultures supports predictions from sexual strategies theory.

Key Words: egalitarian culture, mating strategies, sex differences, Sexual role theory, Sexual strategies theory, sociosexuality

Have sex differences in sexual psychology evolved?

In most psychological traits and abilities, women and men are similar. Most social and psychological differences between the sexes throughout history, whether they have been proposed within the domains of religion, politics, philosophy, or psychology, have proven to be small or nonconsequential. Nonetheless, in some psychological domains the sexes do differ, on average. There are robust differences in prevalence of some forms of psychopathology and overall personality traits. Some of the largest differences, however, fall within the realm of sexual and mating psychology. However, there is considerable debate about what causes these differences.

Sexual strategies theory (SST; Buss & Schmitt, 1993) has guided a variety of research programs investigating sex differences in sexual psychology within evolutionary psychology. SST identified two specific mating strategies within human mating psychology, in which there exists both overlap and differences between the sexes: strategies pertaining to short-term sexual encounters and long-term committed relationships. Largely grounded in parental investment theory (Trivers, 1972), SST offers a metatheory yielding specific predictions related to sex differences in mating orientation and tactics within these distinct domains (Buss, 1998; Buss & Schmitt, 2017). Although both women and men implement both mating strategies, the reproductive benefits of pursuing short-term mates historically have been higher among men producing a stronger preference for short-term mating among men (Buss & Schmitt, 1993). Further, SST predicts what tactics would differ between women and men when competing for mates.

Eagly and Wood (1999; Wood & Eagly, 2003) published critiques of evolutionary perspectives on sex differences, including SST. The primary argument they leveled against findings reported by Buss (1989) on sex differences in mate preferences, a core foundation of SST, was the lack of acknowledgment of potential cultural influences leading to these sex differences. Notably, Eagly and Wood's (1999) social role theory (SRT; see also Buss & Barnes, 1986) emphasized the influence of traditional roles held by women and men in each society and the structural gender inequality they represented. In a reanalysis of the original data from Buss, Eagly and Wood (1999) found covariation between sex differences in mate preferences across cultures and a measure of gender egalitarianism, consistent with SRT.

SRT predicts and seemingly finds diminished sex differences in sexual

preferences in more gender egalitarian societies (e.g. Eagly & Wood, 1999). From an evolutionary perspective, it would seem highly unlikely that psychological mechanisms are not influenced by the selective pressures encountered by women and men in our evolutionary history. This would suggest that while a society becomes more gender egalitarian, there are evolved psychological mechanisms related to biological sex that would still be at play in evaluating partners, derogating rivals, desiring sexual variety, regretting short-term sexual encounters, and so on. SRTs core principle is that sex differences and similarities primarily, if not exclusively, arise from the social roles men and women have in their society (Eagly, 2016).

Thus, the stage is set: Do sex differences in sexual psychology stem from evolved mating strategies that differ across the sexes? Or do sex differences exist despite a fundamental sexual psychology that is monomorphic across the sexes because structural inequality historically and in modern societies gives rise to sex differences? If the first is true, levels of gender equality might or might not be relevant to sex differences, as evolutionary psychological theory acknowledges the possible effects of culture (Gangestad et al., 2006; Walter et al., 2020). However, if the latter is the best description of reality, there will be robust and broad associations between sexual psychology and national level of gender equality; the sexes will become more equal in sexual psychology in more gender equal societies.

Norway as a Natural Lab

Norway, as we will discuss in greater detail, is among the most gender egalitarian nations in the world. There are also other differences between Norway and the United States, aside from gender equality (Bendixen et al., 2017), that are related to gender equality, and especially relevant for studying differences in sexual behavior. US samples are more religious, for instance. Norwegian samples are more sexually liberal.

So, how does Norway fare with regard to gender equality compared to the United States, where studies on sexual psychology from an evolutionary perspective have been criticized for not considering gender roles? The cross-cultural data on measures of gender equality in various societies provide comparisons. The United Nations (UN) has proposed three different measures for quantifying the equality between women and men in different nations (United Nations Development Programme, 1995, 2010).

First, the Gender-Related Development Index (GDI) is based on the indicators of the Human Development Index (HDI), which captures differences

across nations in life expectancy, education, and income. The GDI reflects differences between the sexes in these indicators. A GDI of 1.00, in theory, reflects mean gender equality across the domains. GDI and HDI substantially covary (Klasen, 2006); as such, it is not surprising that Norway at the top of the human development ranking also scores very high on the GDI. Norway has been ranked within the top five since this index was introduced in 1995; its current GDI is 0.993. Due to the correlation with HDI and the influence of life expectancy, it is not an ideal measure of gender equality for comparison between countries.

Second, the Gender Empowerment Measurement (GEM) reflects equality in political participation, income, and participation in the workforce (United Nations Development Programme 1995). Again, Norway has been ranked among the top three countries since the ranking started in 1995 until 2010 (United Nations Development Programme, 1995, 1996, 1997, 1998, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007, 2009). In 2010, the UN introduced the Gender Inequality Index (United Nations Development Programme, 2010), based on concerns that gender empowerment reflects participation in elite activities (e.g., government) and, to a lesser extent, broad inequality across the socioeconomic range. On this index too, Norway has been ranked among top ten countries in the world. In 2018, for instance, Norway ranked fifth. By contrast, the United States ranked forty-second (United Nations Development Programme, 2019).

Third, the more recent Global Gender Gap Index (GGGI), developed by the World Economic Forum, rewards countries that have smaller gender gaps in access to national resources, regardless of the overall levels of resources (Hausmann et al., 2006). As an example, countries are rewarded for equal school enrollment rates but not for overall level of education. Norway has been near the top of the rankings since this index was introduced, never being outside the top three. In 2018, Norway ranked second. By contrast, the United States ranked fifty-first.

Based on the international ratings, Norway has been described as “a haven for gender equality” (Committee on Elimination of Discrimination against Women, 2003), and justly so. Importantly, proponents of SRT (Eagly & Wood, 1999) used two of these international rankings (GDI and GEM) as a proxy for egalitarianism in different societies in the reanalysis of Buss’s data. It is important to note that the measures of gender equality used by Eagly and Wood might not reflect the actual egalitarian ranking at time of Buss’s data collection, as a decade passed between Buss’s paper and Eagly and Wood’s reanalysis. This is also true for some of the comparisons provided in this chapter as the data that

are compared might stem from different years, and hence are not directly comparable when evaluating gender equality measures. Nevertheless, using the historical gender equality measures in more recent studies gives us an advantage. Not only is Norway *currently* among the most egalitarian societies when evaluated on international gender equality rankings, it has been so for the past twenty-five years. This means that adolescents and young adults have lived their entire life in a culture renowned for gender equality, and hence been subjected to cultural influences related to gender equality.

Now, in fact, in no country, including Norway, has complete gender equality been achieved. Norway's GGGI, for instance, currently stands at about 0.85, meaning that it falls 0.15 short of effective equality. Still, it surely reflects greater equality than exists in the United States, where the GGGI stands at .72, 0.27 short of equality—nearly double that in Norway. While SRT, then, should not predict removal of differences in sociosexual traits between women and men in Norway, it surely predicts a substantial reduction in differences between women and men (Bendixen et al., 2015). As Eagly and Wood (1999) explicitly stated, "the sex differences in mate selection criteria that follow from the male-female division of labor should be substantially weakened in societies characterized by greater gender equality" (p. 416).

Norway is thus a natural lab for addressing social role and structural alternative hypotheses to evolutionary theories such as SST. We have employed this for running replications of foundational SST studies (Kennair et al., 2009). Further, our original research on sexual harassment and sexual behaviors in general considered effects of sociosexuality and mating orientation (Bendixen & Kennair, 2017; Botnen et al., 2018; Kennair & Bendixen, 2012). Sex differences in sociosexuality and the predictive power of this construct might also have been predicted to be lower in Norway, if SRT is correct in suggesting that gender equality reduces gender differences.

In the current chapter, we focus on mating strategy research from our lab published the last decade employing sociosexuality and SST. We add relevant research from other Scandinavian countries, which also tend to be characterized by relatively high levels of gender equality, where relevant.

Sexual Strategies *Theory*: A Brief Overview

We provide a very brief overview of SST and its primary predictions examined here (Buss, 1998; Buss & Schmitt, 1993, 2017). SST claims:

(1) That humans have evolved to form long-term pair-bonds that support biparental care. At the same

time, both women and men may opportunistically pursue short-term matings. Hence, both women and men have evolved distinct psychologies shaped to solve adaptive problems faced within long-term and short-term matings, which in part differ across the sexes.

(2) There exists a profound asymmetry in the minimal amount of investment in an offspring across the sexes, owing to women's gestation and lactation of offspring. An opportunistic short-term mating need not cost men much effort and could enhance their reproductive success. Women should be more concerned about whether their partner is committed to and invested in the relationship.

(3) The asymmetry in minimum investment leads to a number of expectations: (a) men will invest more in short-term mating than will women; (b) relatedly, men will pursue sexual opportunities without consideration of commitment and investment from partners more so than will women; (c) men lose more by missing a potential mating opportunity than do women and will regret missing such opportunities more than women; (d) women will regret sex without commitment more often than men; (e) relatedly, women and men will have different negative emotions following short-term sex, with women worrying more about abandonment and men worrying more about detaching from partners.

(4) Because fertilization occurs in women's reproductive tracts, men can be cuckolded—led to invest in offspring not their own—whereas women cannot. Therefore, men's and women's patterns of jealousy in response to potential infidelities will differ. Relatively speaking, men will be more sexually jealous and women will be more jealous of potential abandonment and loss of resources.

Studies have examined pertinent predicted sex differences in these and several other related regards. We will discuss these studies along with studies that examine the size of these same sex differences in Norway.

Interest in Multiple Partners and Short-Term Orientation

A number of predicted sex differences in sexual psychology that follow from SST concern interest in short-term sexual encounters (or, more generally, sex without relationship commitment between partners). Although both women and men should be interested in long-term committed relationships as well, men should be more open to opportunistic sex in absence of commitment, and, on average, have a lower threshold of commitment prior to being willing to engage in sexual relationships. Though not all men may succeed in pursuing short-term partners, some men ancestrally would have increased their fitness through pursuit of multiple short-term partners.

Buss and Schmitt (1993) tested and reported evidence in favor of predictions pertaining to short-term mating interest or interest in sex in absence of relationship commitment in men than in women. These interests may be measured in a variety of ways.

Sociosexuality

Sociosexual orientation or sociosexuality is the willingness to engage in sex

with a partner in absence of emotional closeness and commitment. It can be measured using the Sociosexuality Orientation Inventory (SOI; Simpson & Gangestad, 1991); a revised version was published by Penke and Asendorpf (2008). The latter taps three correlated subcomponents, sociosexual behavior (e.g., number of sex partners in the last year), attitudes (e.g., stated interest in casual sex), and desire (e.g., sexual fantasies about people other than current close partners). Within a closed mating population of equal sex ratio, women and men should report similar mean numbers of actual partners. SST hence predicts the greatest sex differences in attitudes and desire. Schmitt (2005) and later Lippa (2009) both reported robust sex differences across forty-eight and fifty-three nations, respectively, in sociosexual attitudes with men being more unrestricted toward sex without commitment than women. Lippa (2009) reported less restricted sociosexual attitudes in more gender equal nations such as the Scandinavian countries, and particularly so among women, resulting in sex differences being slightly diminished (typically around 0.60 compared to around 0.75 for the US sample and all fifty-three nations combined).

We have collected SOI data as part of several studies, including studies of sexual misperception (Bendixen, 2014; Bendixen et al., 2019), regret (Bendixen et al., 2017; Kennair et al., 2016), and use of dating apps (Botnen et al., 2018). Aggregated across these studies, sex differences in casual sex (SOI behavior) were, not unexpectedly, small. Sex differences in sociosexual attitudes are moderate and very close to those reported in Lippa (2009). However, the sex differences in sociosexual desires are generally large and above 0.80 standard deviation units (see table 11.1 for specifics regarding the attitudes dimension). In one study that directly compared SOI scores in US and Norwegian samples (Bendixen et al., 2017), effects sizes were very similar (for attitudes, $d = 0.60$ vs. 0.63; for desires, $d = 0.96$ vs. 0.79). Overall, however, the sex differences found for sociosexuality in Norway are very similar to the sex differences found internationally (Lippa, 2009; Schmitt, 2005). Therefore, greater gender equality does not seem to lead to smaller sex differences in sociosexuality.

Table 11.1 Comparing Sex Differences across Domains in United States and Norway

	US	**Norway**
Sociosexuality (Attitudes)	0.74[1] 0.75[2]	0.38–0.75[3–7]
Soxiosexuality (Desire)	0.96[5]	0.85[3], 0.79[5], 0.77[7]
Sex differences in mate preferences	0.77 (overall D)[8]	0.75 (overall D)[8]
Age difference first marriage (2000 to date)	1.7–2.4 (U.S. Census Bureau)	2.5–3.0 (SSB)
Reasons for sex (pleasure …)	0.26–0.43[9]	0.03–0.23[10]
Reasons for sex (love …)	0.09–0.13[9]	–0.21–0.35[10]

Being subject to sexual over/under-perception	0.56[11]	0.73[3]
Sexual overperception		0.84 (Men)[4]
Sexual action regret	–0.60[12], –0.32[6]	–0.47[5], –0.41[6]
Sexual inaction regret	0.73,[12] 0.86[6]	0.82[5], 0.71[6]
Post-coital negative emotions (avoidance/neediness intensity)	–0.23, –0.34[13] (Women) 0.09, 0.13[13] (Men)	0.00[13] (Women) 0.51[13] (Men)
Jealousy responses (forced choice)	1.01 (Scenarios 1–4)[14]	0.86[16], 0.87[17]
Jealousy responses (continuous)	0.31[15]	0.86[17]
Derogation and self-promotion	Table 7[18]	Table 7[18]

Note. D = Mahalanobis distance; SSB = Norwegian Statistics.

[1] Schmitt (2005),

[2] Lippa (2009),

[3] Bendixen (2014),

[4] Bendixen et al. (2019, Study 1),

[5] Kennair et al. (2016),

[6] Bendixen et al. (2017),

[7] Botnen et al. (2018),

[8] Walter et al.(2020),

[9] Meston & Buss (2007),

[10] Kennair et al. (2015),

[11] Haselton (2003),

[12] Galperin et al. (2013, Study 3),

[13] Fernandes et al. (2016),

[14] Carpenter (2012),

[15] Sagarin et al. (2012),

[16] Bendixen et al. (2015a),

[17] Bendixen et al. (2015b),

[18] Bendixen & Kennair (2015).

Interest in Short-Term Sex and Ideal Number of Partners

Buss and Schmitt (1993) did not test SST using the SOI itself. Rather, they asked women and men (1) how much they were interested in short-term and long-term sexual relationships, (2) their ideal number of sexual partners, and (3) the time interval after the onset of a relationship that individuals would be willing to have sex. Their sample was strictly a sample of US college students. We assessed these same features in samples of Norwegian college students.

Figures 11.1–11.3 illustrate the overlap between findings from Buss and

Schmitt (1993) and Kennair et al. (2009), which compares findings more than a decade apart and two nations that differ in egalitarian, sexually liberal and secular attitudes. Figure 11.1 reports current interest in short-term and long-term relationships. In both nations (Norway in gray), women, on average, indicate a clear preference for long-term relationships over short-term relationships in both nations. Norwegian men express a near-equal interest in both types of mating strategies, while US men, on average express preference for a short-term partner. Still, the gendered patterns of preference are similar across Norway and the United States.

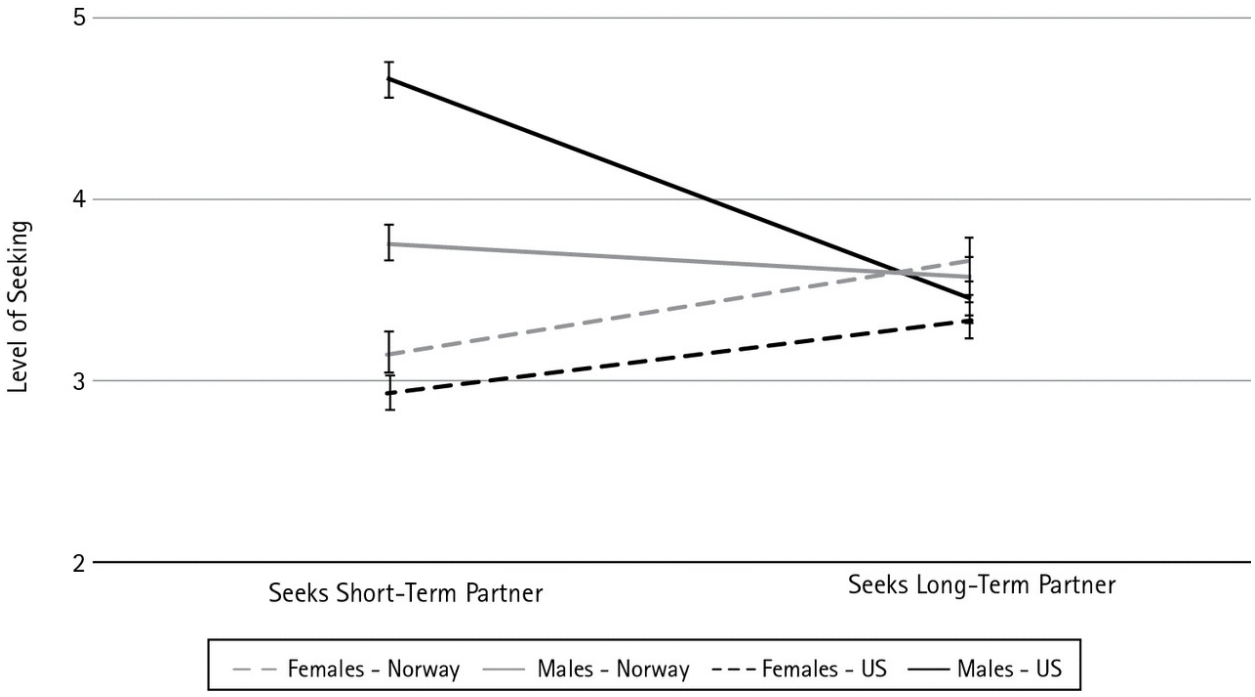

Figure 11.1 Current interest in short-term and long-term relationships. Norwegian data in gray (Kennair et al., 2009), US data in black (Buss & Schmitt, 1993).

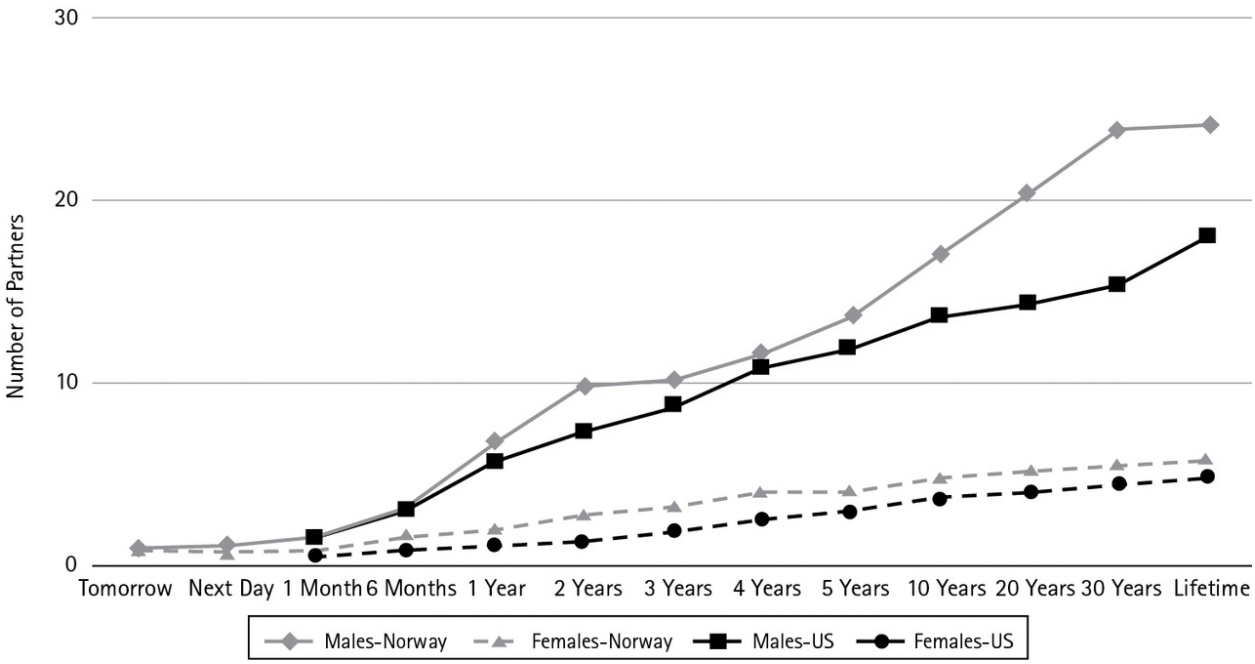

Figure 11.2 Number of partners desired with time. Norwegian data in gray (Kennair et al., 2009), US data in black (Schmitt & Buss, 1993). Male data in solid lines. Female data in dashed lines.

In sum, sex differences in various measures of interest in and willingness to have sex in absence of commitment are robust in Norway, just as they are in the United States and elsewhere (e.g., Lippa, 2009; Schmitt, 2005). Are they weakened in Norway, as might be expected by SRT? The answer is complicated by the fact that relative sex differences, compared to the United States, depend on the precise measure. Norwegian men express less interest in short-term sex than do US men—*yet*, they also claim a *greater* ideal number of lifetime sexual partners. Norwegian women are willingly to have sex after less commitment and passage of time compared to US women—*yet*, we see evidence of little difference is their interest in short-term sex and ideal number of partners. If the size of a sex difference in interest in short-term sex differs across Norway and the United States, it is nuanced and measure-dependent.

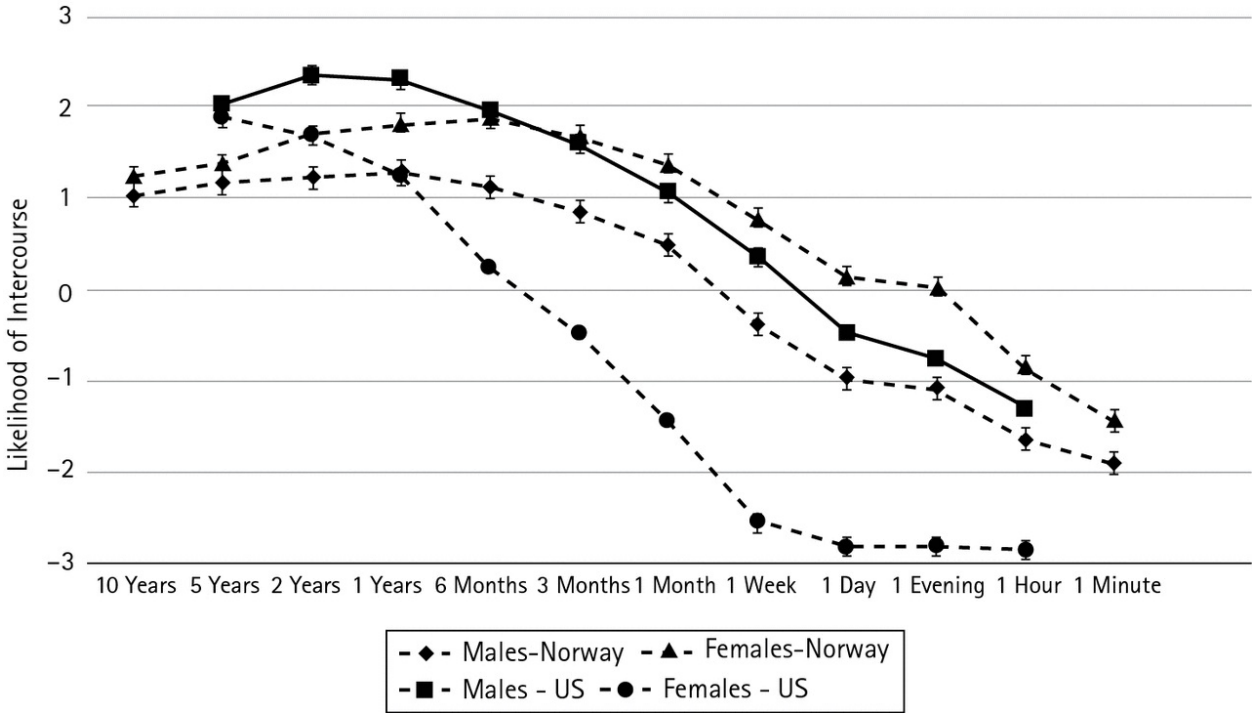

Figure 11.3 Time preferred to have elapsed before having sex with a sexually attractive partner.

Partner Preferences

Age preferences have been extensively studied in light of evolutionary psychology since Buss's (1989) cross-cultural analysis. Buss predicted that men would prefer women in their early twenties as age is a cue for current fertility and future reproductive value (Buss, 1989). Women have been hypothesized to show preferences for somewhat older men, as social status and resource attainment are linked to age for men. The sex difference in age preferences has later been found to replicate both in various cultures (e.g., Dunn et al., 2010) and across time (for a review on age preferences, see Conroy-Beam & Buss, 2019). One particularly interesting study of adolescents found men in their late teens showing a preference for slightly older women, in line with predictions from an evolutionary approach linking age to fertility, and seemingly at odds with a cultural prediction of men wanting a younger partner that fits the male breadwinner/female homemaker roles (Kenrick et al., 1996). We therefore investigated a Norwegian sample to investigate how growing up in a very gender egalitarian society influenced age preferences. In sample of 1,076 participants, strong evidence emerged for sex differences in both age preferences and age of current partner (Grøntvedt & Kennair, 2013).

As age increased, the difference between women and men's preference

increased, and the difference was in effect caused by men progressively preferring a younger partner than themselves. Effect sizes between the three age groups (eighteen to twenty, twenty-one to twenty-three, and twenty-four to thirty) for both ideal long-term partners (d = 1.18, 1.61, and 1.73) and ideal short-term partners (d = 0.98, 1.32, and 1.61) were large. In accordance with SST, men's age preferences where consistent with women's fertility. For the men in the youngest age group, this was reflected in the preference for slightly older partners than themselves and close to peak fertility in early twenties as previously indicated (e.g., Kenrick et al., 1996). And in accordance with previous findings on marriage (e.g., Kenrick & Keefe, 1992), men in the sample were in relationships with younger women, and women with older men. In fact, the mean age of first marriage in Norway is two and a half to three years lower for women than for men, and although age of first marriage has increased steadily since the 1970s, the sex difference in age has been consistent (Statistics Norway, 2019). The results are also in line with more recent cross-cultural evidence of sex differences in partners age (Walter et al., 2020).

A previous study from the relatively egalitarian nation of Netherlands (Buunk et al., 2001) found evidence for larger sex differences in lowest age preferences in more sexual relationships and sexual fantasies compared to age preferences in long-term partners such as marriage, driven by the fact that when men become older they desire considerably younger partners compared to themselves in short-term settings. Women in their fifties and sixties might have sexual fantasies about men close to their own age, whereas men in these age groups fantasize about women in their late twenties to early thirties. We did not find this same difference, but it should be noted that age in our sample's age range was rather limited and consisted of young adults in their late teens and twenties. Overall, even in a more gender egalitarian nation like Norway, there seem to be strong sex differences in age preferences.

Reasons for Sex

Based on free responses, Meston and Buss (2007) catalogued 237 reasons why women and men have sex. In a structured survey, some reasons were rarely endorsed, but thirteen subfactors were identified through factor analyses—for example, sex for physical pleasure, sex driven by sexual attraction, sex as experience-seeking, sex for resources, sex for status, sex as revenge, sex for love or commitment, and sex as expression of intimacy. Sex differences in rates of endorsement were common. Men more strongly endorsed reasons pertaining to physical attraction to a partner, physical pleasure, status seeking, and simply

because an opportunity presented itself. Women endorsed very few reasons more than men; they claimed to have sex more out of love (though on a factor composite, there emerged no significant difference on this dimension). To investigate whether sex differences are similar in Norway, we administered a Norwegian version of Meston and Buss's survey to 1,372 participants (64.4 percent women) between 2006 and 2009 (Kennair et al., 2015). We identified a similar pattern of Meston and Buss's thirteen basic factors of reasons for sex. Unlike Buss and Meston, we split both women and men into groups exclusively interested in long-term sexual relationships and those seeking short-term sexual relationships at least to some extent. Some nation-level differences emerged. Norwegian women and men more strongly endorsed pleasure and sexual attraction to a partner as reasons than did Meston and Buss's US sample. Norwegians endorsed at lower rates reasons pertaining to gaining resources, status, revenge, or other utilitarian reasons. Lest one think that Norwegians are simply more sexually permissive, however, Norwegians also endorsed at higher rates reasons pertaining to love and commitment. Sex differences generally ran in the same direction as the US sample. Sex differences in motives for pleasure, sexual attraction, and experience-seeking were smaller than in the United States (*d*'s ranging from 0.03 to 0.23 vs. 0.26 to 0.43 in Meston and Buss's study). At the same time, however, sex differences in engaging in sex for love and commitment were larger in Norway: Norwegian women were more likely to endorse reasons related to love and expression of intimacy (d = -0.21 to -0.35), in contrast to Meston and Buss's study, in which men still endorsed these reasons slightly more (d = 0.09 to 0.13). Although there seem to be similar patterns in reasons for sex both in US samples and in the Norwegian sample, there are some differences. In Norway, smaller sex differences were found for motives of pleasure, sexual attraction and experience-seeking, whereas there were larger sex differences for reasons such as love and expression of intimacy—which might be more in line with SST than the original findings.

Sexual Initiative and Response

Several studies report that men initiate sexual interactions more than women (e.g., Baumeister et al., 2001; Byers & Heinlein, 1989). Further, relative to women, men would prefer to have more frequent sex in their relationships, and fewer are satisfied with their frequency of sex (Heyman et al., 2009; Smith et al., 2011). In Norway, Kennair et al. (2009) found similar sex differences. In another sample of 759 Norwegian participants (Grøntvedt et al., 2015), men initiated sexual intercourse about two times more than women (OR = 1.93); when in

long-term relationships, men initiated sex more than three and a half times more often than women (OR = 3.51).

In a famous examination of receptivity to explicit and blatant sexual invitations, with no prior relationship, Clark and Hatfield (1989) had confederates approach and proposition strangers on campus. In two independent studies, carried out four years apart (before and during the early outbreaks of the AIDS epidemic), 75 percent and 69 percent of the men consented, respectively; no women consented. Sex differences were also very strong for requests to "come to my place," while no sex difference was evident for requests to go "on a date." Twenty years later, a Danish study addressed the same question in a direct replication (Hald & Høgh-Olesen, 2010). As in the original studies, moderately attractive confederates approached 216 women and 173 men. As in the original studies, no women accepted invitations to "go to bed with me"; 59 percent of single men did (d = 1.66). As well, men were more likely to accept an invitation to "come to my place" (among singles: women yes 21 percent, men yes 40 percent, d = 0.41). Subjects' willingness to have sex was moderated by relationship status; singles were more likely to respond positively to going on a date and the more sexual invitations. Only women participants' receptivity to going on a date was moderated by the confederates' attractivity.

Overall, samples from the United States and Norway were similar when it came to desired frequency of sex and initiation of sex in a relationship. Furthermore, both in the United States and a more gender egalitarian nation such as Denmark, women were less likely to engage in invitations to short-term sexual relations.

Sexual Over- and Underperception

Women's reproductive output is far more constrained than men's (Trivers, 1972). Although most mammalian females have limits imposed on them by the costs of gestation and offspring care in terms of time and energy, male constraints are limited by the number of females they can mate with. While humans cross-culturally engage in long-term relationships with biparental care, an increase in matings with fertile partners other than long-term committed partner could increase the biological fitness of men but not for women (Buss & Schmitt, 1993). Hence, men are more willing to have casual, uncommitted sex than women. These sex differences also manifest in systematic biases in interpretation of signals that may convey cues to sexual interest in opposite-sex encounters. Error management theory (Haselton & Buss, 2000; Haselton & Galperin, 2013; Haselton & Nettle, 2006) applies principles of signal detection

theory (Green & Swets, 1966; Swets et al., 2000) to propose that selection may have engineered psychological adaptations for judgment under uncertainty that produce more errors overall but fewer costly errors. In particular, nonverbal cues from an opposite-sex individual such as eye contact, smiles, open postures, or physical touch may convey either sexual interest or mere friendliness. Men overperceive sexual interest presumably because missed sexual opportunities (i.e., false negatives) are (or have been ancestrally) more costly than wasted efforts or reputational costs associated with false positives/false alarms. For women, missed opportunities would have been less costly, meaning sexual overperception bias is expected in men but not in women.

This effect has been shown across studies using different methodology, ranging from videotaped meetings and observations of speed-dates between women and men, to questionnaires involving judgment of women and men's intentions, and reports of past naturally occurring encounters of opposite-sex meetings. The latter methodology was used by Haselton (2003) showing that far more female than male students (and at a higher rate) reported being subject to sexual overperception during the past twelve months (i.e., their intentions were misperceived).

Bendixen (2014) performed the first direct replication of Haselton's (2003) study ten years later using a Norwegian student sample of 181 women and 127 men. Despite the time lag and the cultural differences between samples from the United States and Norway in terms of politics, religiosity, and sexual liberalism, Bendixen's findings mirrored those in the original study, though in Norway the sex difference was greater: Compared to men, women were markedly more subject to sexual overperception relative to underperception. Specifically, women reported far more overperception than men (interaction effect: $d = 0.73$), a sex effect slightly stronger than in the original study (interaction effect: $d = 0.56$). Moreover, and similar to the original study, sociosexual attitudes affected the overall level of being misperceived (over- and underperception). More frequent misperception was reported by sexually unrestricted participants. Finally, sexually unrestricted participants reported more false alarms (overperception more than underperception) than restricted participants.

As a follow-up to Bendixen (2014), two studies (Study 1: $N = 224$, 67 percent women; Study 2, $N = 211$, 64 percent women) examined misperceptions of sexual intent in opposite sex encounters and tactical signaling of own sexual attraction using self-reports from naturalistic dating contexts (Bendixen et al., 2019). The second study was carried out to replicate the first, but in a context of ample mating opportunities (i.e., during freshmen weeks). A strong effect of male sexual overperception was found in Study 1 ($d = 0.84$). Because single

freshmen women in Study 2 reported high levels of sexual attraction compared to non-freshmen women, this effect was not replicated for the sample as a whole, only among non-freshmen women. As well, the studies were designed to particularly test if male overperception bias could be a result of women acting coy (playing hard-to-get) or strategically downplaying signals of sexual attraction; no indication of this was found in either study. In sum, both in the United States and the more gender egalitarian Norway, sex differences were largely similar; men tended to overperceive sexual attraction in both nations.

Sexual Regret and Postcoital Negative Emotions

Regret is both a counterfactual cognitive process as well as an emotion (Kennair & Bendixen, 2018; Roese et al., 2006). It arises when, in retrospect, one considers how it would have been better if one had chosen a different course of action than that chosen. Action regret occurs when one wishes that one had not acted as one did; inaction regret occurs when one refrained from doing what one in retrospect should have done. As sexual decisions are fundamental to reproductive success, a central domain of regret concerns sexual behavior, especially in the short-term or casual sex domain (Kennair et al., 2016). Interestingly, only the romantic domain evinces sex differences in regret differences (Roese et al., 2006). Galperin et al. (2013) suggested that regret is an evolved mental mechanism designed to reduce future maladaptive sexual behavior, based upon aversive emotional processing of poor past choices.

From the perspective of SST, the sexes should differ with regard to sexual regret (Bendixen et al., 2017; Galperin et al., 2013; Kennair & Bendixen, 2018; Kennair et al., 2016; Kennair et al., 2018). Due to the obligatory parental investment (Trivers, 1972), women should be particularly sensitive to the costs of pregnancy. Women may especially regret casual sex, which ancestrally risked pregnancy by a subpar male or without a committed, investing partner. By contrast, men have regretted having passed up casual sexual opportunities. Throughout evolutionary history, it is sexual access that has been the fitness bottleneck for men (Karmin et al., 2015).

Consistent with these ideas, in a North American sample, Fisher et al. (2011) found that women more than men regretted having had casual sex. And Roese et al. (2006) found that men more than women regretted missed sexual opportunities. According to Eshbaugh and Gute (2008), it was reproductively relevant sexual behavior (i.e., sexual intercourse) that elicited regret. In a subsequent single study, Galperin et al. (2013) found both increased casual sex action regret among women and increased casual sex inaction regret among men.

We have conducted three studies examining sex differences in sexual regret in Norwegian samples (Bendixen et al., 2017; Kennair et al., 2016; Kennair et al., 2018), as well as various factors that may explain the difference. With a Norwegian student sample (N = 263, 64 percent women), Kennair et al. (2016) replicated Galperin's findings: There was a clear sex difference (Action regret: women more than men, d = 0.47; Inaction regret: men more than women, d = 0.82). As proposed by Galperin et al. (2013), differences in men and women's gratification from sex (sexual pleasure, orgasm, orgasm importance) statistically accounted for the sex difference in action regret. Still, the most physically gratified women regretted short-term sex more than the least gratified men. Bendixen et al. (2017) simultaneously examined US (N = 466) and Norwegian (N = 853) samples. Once again, effect sizes were similar to Galperin et al.'s study (see table 11.1). Religiosity positively and sociosexuality negatively predicted regret and partially explained a mean difference in regret across nations. However, sex was the most powerful predictor within and between nations. Furthermore, and importantly, the similarity of effect sizes of the sex difference across nations suggest little to no impact of gender equality.

Kennair et al. (2018) addressed in further detail different possible proximate predictors of the robust sex difference in level of regret in their most recent casual sex encounter (a subsample of the above). We examined the relevance of several more possible predictors such as gratification, worry, disgust, sexual competence, sexual pressure, and initiative to sex, in the United States and Norway. Yet again, sex is the major predictor of type of regret. However, for women, taking the initiative to sexual relations reduced action regret for most recent casual sex encounter. These women most likely desired casual sex more.

While the three studies on regret all replicate predicted sex differences, they do not address an important aspect of the evolutionary function of regret, as suggested by Galperin et al. We do not yet know whether regret has any adaptive effects on future sexual decision making—however, the first test of this hypothesis did not provide support that regret influences behavior adaptively (Kennair, 2021,).

Postcoital Negative Emotions

Associated with sexual regret is the phenomenon of postcoital negative emotion. Fernandes et al. (2016) identified three factors underlying ratings of a number of aversive feelings postcoitus, two of which they predicted and found to be sex-differentiated based upon SST. Relative to men, women reported higher intensity and frequency of aversive emotions associated with feeling abandoned

(reporting feelings such as Need to be comforted, Feeling of worthlessness, Tearfulness or feeling like crying, and Feeling of helplessness), where abandonment would have been associated with loss of male investment in offspring ancestrally. Men, by contrast, more intensely and frequently expressed desire to detach or leave their partner (reporting feelings of Irritability, Anger, Disgust for partner, and Need to be alone); ancestrally, males could at times benefit from pursuing yet additional mating opportunities. The patterns of postcoital negative emotions found by Fernandes et al. (2016) thus suggest that this phenomenon can be understood as adaptive from an SST perspective, rather than as a dysfunction or pathology. There were four samples in this study (Brazilian, Midwestern-American, Anglo-American, and Norwegian), all showing similar patterns of response, but Norwegian women reported lower levels of need for need to bond compared to women in the three other samples. This may be a result of greater sexual liberalism and cultural differences in Norway.

Jealousy Responses

The adaptive functions of jealousy are similar for women and men with regard to warding off potential mate poachers and preventing relationship defection (Buss, 2013). However, women and men have faced different adaptive problems regarding infidelity. The adaptive problem of cuckoldry is faced only by men who invest in offspring while the adaptive problem of maintaining resources has been faced primarily by women. This would produce adaptations where men are particularly sensitive to sexual forms of infidelity as opposed to emotional forms relative to women (Buss, 2013). Female infidelity has been a recurrent feature of human evolutionary history, and because fertilization and gestation are internal, this increases paternal uncertainty and the possibility of being cuckolded (Goetz & Shackelford, 2009). How common extra-pair paternity is and has been in traditional societies is a matter of debate. In some societies, it may be as rare as a percent or two of all births; in other societies, it may be more common (Anderson, 2006).

Cuckoldry is costly for men investing in offspring production, and, hence, one should expect adaptations that lessen the probability of cuckoldry or reduce its costs. Two major forms of infidelity have been identified: having an extra-pair encounter or affiliation that is merely sexual (sexual infidelity), and falling in love or becoming attached to an extra-pair partner (i.e., emotional infidelity) and committed to an extra-pair partner. Both forms represent a threat to a valued relationship, and either form may activate a jealousy response.

However, these sex-differentiated responses may be sensitive to male investment across cultures. In cultures where male investment is high (or expectedly high), sex differences may be particularly strong (Buss et al., 1992). The Scandinavian countries seem to provide the ideal context for examining this hypothesis because of the high male investment in childcare in terms of time and resources (formal regulations and economic compensation for parental leave).

Four studies have been published on jealousy responses using Scandinavian samples. The first is a Swedish study of 376 (54 percent women) university college students (Wiederman & Kendall, 1999). They measured women and men's jealousy responses using a single forced-choice scenario describing one's partner being either sexually or emotionally unfaithful. More than 61 percent of men and 37 percent of women reported being more upset by imagining their partner being sexually unfaithful. Their finding was very similar to a prior study of a US sample using the same scenario. The second study by Kennair et al. (2011) of 506 (60 percent women) Norwegian university students, applied two scenarios adapted from Buss et al. (1999). For both scenarios, the authors found that 50 percent of the men and 20 percent of the women found the sexual aspects of the infidelity more upsetting. The same two scenarios were used in a later study of Norwegian university students (N = 480, 46 percent women) (Bendixen et al., 2015b). Women and men's responses to the two scenarios were very similar to those in Wiederman and Kendall (1999), with a mean sex difference (Cohen's d = 0.86). These sex differences are very similar to those reported from various US student samples as shown in table 11.1 (Carpenter, 2012). In a fourth and final study of 1,074 (59 percent women), university students (Bendixen et al., 2015a) expanded the number of scenarios to four to increase reliability, and also included continuous measures for jealousy responses. The participants were randomly assigned to type of measurement (forced choice and continuous measure) along with question order manipulation as in the latter study. The sex difference in what aspect of the infidelity that was more upsetting was large in both measures (forced choice: d = 0.87; continuous measures: d = 0.86) (see also Edlund and Sagarin, this volume). Relative to women, men were moderately more upset by sexual infidelity than by emotional infidelity. These sex differences were not reliably moderated by relationship status or commitment, age, or individual differences in sociosexuality, but partnered individuals reported greater levels of jealousy on continuous measures compared to single individuals. Women were moderately more distressed when imagining their partner being emotionally unfaithful than being sexually unfaithful.

Overall, the sex differences were similar in the United States and Norway, as in both nations, women tended to find scenarios of emotional infidelity more

upsetting whereas men were more distressed by scenarios of sexual infidelity.

Derogation and Self-Promotion

One of the major contributions of SST is the distinction in sexual competition for mates for short-term sex and long-term relationships. This includes various competitor derogation tactics and self-promotion tactics (Schmitt & Buss, 1996). Derogation tactics are attempts to reduce a competitors' perceived mate value (e.g., by commenting on their flaws and bad qualities or to dominate them in various ways). Self-promotion stresses one's own qualities in an attempt to increase one's perceived mate value relative to others (e.g., by signaling physical attractiveness, sexual availability, and sexual exclusivity; Bleske-Rechek & Buss, 2006; Buss, 1988; Schmitt, 2002; Schmitt & Buss, 1996). Some tactics that are efficient for competing for long-term mates (e.g., signals of sexual exclusivity) are predicted not to be efficient in competition for short-term sexual encounters (one-night stands) (Schmitt & Buss, 1996). Furthermore, the efficiency of tactics is highly contingent upon the sex of the actor (Schmitt & Buss, 1996).

Bendixen and Kennair (2015) aimed to replicate Schmitt and Buss's (1996) findings in Norway. Study 1 focused on self-promotion (N = 270, 51 percent women), and Study 2 on competitor derogation (N = 350, 58 percent women) adding sociosexuality as a moderator. The study design was between-subjects, as contrasted with the mixed design used by Schmitt and Buss. In line with the SST predictions, the findings showed both sex differences as well as differences between short-term and long-term contexts. For example, using cues of sexual availability were most effective for women in short-term contexts, compared to women in long-term contexts and men. Tactics involving cues to sexual exclusivity were judged most effective when used by women in long-term contexts. Acting dominant was judged more effective when used by men. Resource signaling tactics showed no sex differences. Tactics that involved cues to love, commitment, and derogating a rival for their exploitativeness were much more effective when used in long-term contexts and for men. Derogatory comments about one's rival's attractiveness were generally not considered to be an efficient tactic. Overall, not only was the Norwegian study able to replicate twenty of the twenty-four specific tests and six of the seven hypotheses from the original study by Schmitt and Buss (1996); the effects were largely comparable to those of the original study. In addition, we found that sociosexuality was associated with effectiveness ratings of sexual availability and surgency (more effective among unrestricted participants) and fidelity, love, and commitment

(more effective among restricted participants). These findings have recently been replicated again in a similar study on flirtation tactics (see Kennair et al., 2022).

Discussion

We set the stage at the outset of this overview. SST expects that sex differences relating to a variety of facets of, broadly speaking, mating will be robust, though variations as a function of socioecology may exist. SRT explicitly expects that sex differences in mating will be lessened in cultures that are gender egalitarian, relative to others. As no nation on earth currently exhibits perfect gender equality with regard to access to resources and expression of influence, SRT may not expect a complete absence of sex differences in even the most egalitarian nation due to the lingering effects of traditional social roles. But clearly, sex differences in a relatively gender egalitarian country should be systematically weaker, compared to less gender egalitarian countries. For decades, Norway has been recognized as one of the most gender egalitarian countries in the world. Over the past decade and more, we have sought to programmatically answer a key question: Are sex differences predicted by SST in mating domains systematically smaller in Norway, as compared to other places, notably the United States, where most of the original work was conducted?

The aggregate results of many studies collectively involving thousands of participants yield a clear answer: No. Effect sizes across a number of domains are summarized in table 11.1. As we described earlier, studies assessing sex differences in interest in sex outside committed relationships yield no clear pattern. Sex differences in sociosexual attitudes and desires may be slightly larger in US samples as compared to Norway, perhaps owing to Norway being more sexually liberal and less religious (Bendixen et al., 2017). At the same time, sex differences in desired number of partners are actually somewhat greater in Norway. Sex differences in reasons for sex related to pleasure and partner attractiveness are somewhat smaller in Norway. But again, sex differences in reasons for sex related to love and commitment—where women are more likely to endorse these reasons—are actually more strongly in line with expectations of SST in Norway compared to the United States. Sex differences in sexual overperception bias, purportedly driven by interest in expanding sexual opportunities, are similarly somewhat stronger in Norwegian samples. Sex differences in sexual regret over uncommitted sex as well as missed sexual opportunities are comparable in US and Norwegian samples. And patterns of postcoital negative emotions are not systematically stronger in the United States

relative to Norway. Finally, sex differences in patterns of sexual versus emotional jealousy are not systematically different—and, indeed, continuous ratings measures that purportedly offer more stringent tests of sex differences have yielded larger sex differences in Norway. There is simply no domain in which one could argue that, clearly, Norwegians systematically display less robust or absent differences across the sexes.

Table 11.1 also lists outcomes of research we have not reviewed here generally examining mate preferences. Walter et al. (2020) found that the overall multivariate D reflecting sex differences in mate preferences was nearly identical in the United States and Norway (0.77 vs. 0.75).

This is not to deny that there could exist some more subtle, domain-specific differences in sexual differentiation. The fact that Norwegian women report themselves to be interested in the pleasures of sex almost as much as Norwegian men, while also clearly claiming to be more interested in sex as a mean of expressing and solidifying love and commitment (and more so than in a large US sample) is interesting and perhaps worthy of further empirical investigation and interpretation. But these patterns are not consistent with expected sex differences being weaker in Norway as opposed to the United States. Rather, they hint at the possibility that relative sex differences across countries may vary across measures. It might also be that relevant cultural differences in sexual liberalism and lack of religiosity influences sexual behaviors more than specifically gender equality does.

It is important to note that culture is expected to have effects from an evolutionary perspective (such as, for instance, sex ratio or extrinsic mortality risks; see, e.g., Gangestad et al., 2006). The belief that evolutionary perspectives dismiss effects of culture or ecology is a myth and a simplification of the nature–nurture debate. Evolved human universals exist, but they will be expressed to a higher or lower degree, depending upon relevant ecological features. Further, one expects measurable, observable sex differences from an SRT perspective. It is the explanation of these differences and the magnitude of differences in more gender egalitarian versus less gender egalitarian cultures that differs between the two theoretical perspectives. From an evolutionary perspective, one does not need to expect effects largely driven by social roles. Rather, one might expect effects are a function of other variables that affect key elements of relationship dynamics (e.g., the value of short-term relationships, the value of paternal investment, the value of investment in offspring quality vs. quantity, and sex ratio).

Some, but not all, the studies reviewed in this chapter are direct replications. Also, some effects have been examined in single studies. There are therefore

limits to the generalizability of the findings and comparisons. Nonetheless, the findings presented in this chapter dovetail nicely with a recent large international replication by Walter et al (2020). For some areas, such as jealousy and regret, the results are robust across several studies. Findings in other areas (e.g., reasons for sex), while being closer to SST predictions in Norwegian data, warrant further investigation. We also advocate future research aimed at developing better international measures that may address cultural differences that can explain variation in sexual psychology, including sexual liberalism and secularism.

Sexual Strategies Theory is the best predictor of sexual psychology in an egalitarian culture

Based on the Lakatosian criteria for evaluating theories, a research program is evaluated as "good" when it is theoretical progressive, yielding novel, specific, testable predictions and overcoming empirical anomalies that emerge (Ketelaar & Ellis, 2000). A successful theory, then has explanatory power; it explains findings or can adjust to do so (Lakatos, 1978). SST provides a framework that offers specific predictions. Over the past decade, several replications and novel studies from Norway—a progressive, secularized, sexually liberal, and gender egalitarian society—have provided support for SST. Neither the currently reviewed research nor Walter et al.'s (2020) recent large-scale investigation of effects of gender equality on partner preferences support the idea that humans possess a sexually monomorphic mating psychology that is primarily influenced by levels of structural gender equality or gender roles within the society in which it has been studied. SRT specifically predicts marked reduction in sex differences in more gender egalitarian societies. And since completely gender egalitarian societies do not yet exist (at least based on the international measures presented here), the historical and current levels of gender equality in Norwegian society render the presented data the best available tests of predictions from SRT. Most of the data above are from subjects born and raised in one of the world's most gender egalitarian society and thus being subjected to its cultural influences throughout their entire life, another reason that these data offer the best available tests to date.

Social psychology is in dire need of theories that make predictions, organize data, and provide us with the basis of data-driven cumulative theory development. The current dismal scientific state with ad hoc principles and nonreplicable findings needs to be addressed. Nonreplicated findings and results

from single studies may not offer true insights. Recent, large-scale replications (e.g., Walter et al., 2020) and the current studies of mating strategies suggest that gender egalitarianism is not a fundamental explanatory feature of mating psychology. The robust finding is that the best predictor of sexual psychology in Norway is SST, and at an individual level the related notion of sociosexuality.

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CHAPTER 12

Mating Strategy Variation by Sexual Orientation

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Abstract

There is tremendous variety in the sexual behaviors and mating strategies observable across individuals, genders, cultures, populations, and ecologies. One critically important variation in mating strategies among human and nonhuman animals is the extent to which they are interested in engaging in same-sex sexual behaviors and relationships. Same-sex sexual behavior has been observed in many species of mammals, including primates. Here, we focus primarily on sexual orientation and mating in humans. Specifically, we review different ways to conceptualize sex, gender, and sexual orientation and the widespread examples of same-sex sexual orientations and behaviors seen across cultures and across history. We then turn to the associations of sexual orientation to different mating behaviors and preferences, including sociosexuality and consensual nonmonogamy and preferences for physical characteristics, age, and other traits such as status and income. We also highlight mating preferences often considered by LGBTQ people when seeking mates, such as masculinity or femininity of potential partners and behavioral repertoire preferences (e.g., insertive or receptive sexual partners). Finally, we examine some of the evolutionary perspectives that have been offered to explain same-sex sexual behavior from an adaptationist or a by-product perspective. Overall, this review highlights the importance of considering the environmental, social, ecological, and evolutionary factors that concomitantly impact sexual orientation and the mating strategies of people across diverse LGBTQ identities.

Key Words: sexual orientation, mating strategy, evolution, gender, mate preferences

There is tremendous variety in the sexual behaviors and mating strategies observed throughout the animal kingdom. One critically important variation in mating strategies among human and nonhuman animals is the extent to which they engage in *same-sex sexual behaviors*. Bagemihl (1999) highlighted examples of these behaviors among hundreds of species, including dolphins, deer, zebras, giraffes, birds, sheep, and elephants in the wild and in captivity. It has been observed in many species of birds, with one well-studied example being albatrosses. As many as one third of females form same-sex pairings and assist each other with the raising of chicks, which has reproductive benefits for the females in these relationships (Young & VanderWerf, 2014).

The same-sex behavior and pairings among primates are of particular interest. Sommer and Vasey (2006) provided detailed chapters examining same-sex sexual behavior in many species of primates, including bonobos, rhesus monkeys, langur monkeys, gorillas, and Japanese macaques. For example, female Japanese macaques exhibit courtship behaviors directed toward other females, and engage in vulvar, perineal, and anal stimulation with other females. Perhaps the most well-known example among primates is the genito-genital rubbing, fellatio, and manual stimulation commonly observed among bonobos with same-sex and cross-sex partners.

Looking to humans, it is clear that same-sex sexual behavior and relationships have existed in human cultures across the world and throughout human history (Kirkpatrick, 2000). A rather substantial literature on same-sex sexual behaviors has emerged, particularly with a focus on sexual health and sexually transmitted infections. Research on many aspects of sexual orientation have received extensive attention (for a review, see Bailey et al., 2016), but research mate preferences across sexual orientations has been surprisingly limited until recently.

In this chapter, we first describe various definitions of sex, sexual orientation, and gender. We then review how mating strategies and mate preference vary by sexual orientation. Finally, we focus our attention on some of the evolutionary perspectives that have been offered to understand how same-sex sexual attraction emerges and is maintained within populations.

Defining Sex, Gender, and Sexual Orientation

Defining and measuring sex, gender, and sexual orientation can be challenging, because these are all concepts with fuzzy boundaries. In this section, we discuss some of these challenges, and how these challenges can impact our understanding of the prevalence of different sexual orientations and the mating behaviors connected to these orientations.

Defining Sex

When we think of sex, there is a constellation of traits that are often associated with defining male versus female. We can focus on *male-typical* versus *female-typical chromosomal sex* (XY vs. XY), *genetic sex* (SRY genes present vs. absent), *gonads* (testes vs. ovaries), *gametes produced* (sperm vs. egg), *internal reproductive system* (Wolffian vs. Mullerian ducts), *hormone levels* (testosterone and estrogen), *external genitals* (e.g., penis vs. vulva), *brain structures* (masculinized vs. feminized), and *secondary sex characteristics* (e.g., facial hair vs. breasts). For many people, all of these traits align in the male-typical or female-typical direction, but this is not the case for people who are *intersex* (Vilain, 2006).

Although there are many ways in which we can examine sex, choosing the best approach is dependent on the topic at hand. Many biologists define sex based on gamete size, with males having the smaller and females having the larger gametes (Garcia-Gonzalez et al., 2013), but attraction to people who produce sperm versus eggs would not map well onto our general understanding of what constitutes a person's sexual orientation. Furthermore, attractions to the many of the different variations of body types within the category of *intersex* and *transgender* are not easily grouped within the often-used categories of gay/lesbian, bisexual, or heterosexual.

Defining Sexual Orientation

One very broad definition of *sexual orientation* is the emotional or erotic attraction to a particular sex or sexes (Gonsiorek et al., 1995). Furthermore, sexual orientation is not a static experience for some people: their sexual orientations can fluctuate notably over short and long periods of time. Much of the existing research assesses orientation using the self-reported identities of "heterosexual/straight" (someone exclusively attracted to those of the other sex) "homosexual/gay/lesbian" (someone exclusively attracted to those of the same sex) and "bisexual" (someone who is attracted to both the same and other sex). Because these labels are up to interpretation, they often do not account for the full range of attractions and behaviors that an individual has and groups

dissimilar people into one broader category. For example, someone may identify as heterosexual but also have attractions to members of the same sex and occasionally have sexual relationships with members of the same sex.

In order to reduce this complexity, we could try to limit the definition of sexual orientation to just one key dimension depending on the purpose of the research. For example, public health researchers interested in links between sexual behavior and risk for sexually transmitted infections might focus their attention specifically on sexual behavior, such as identifying "men who have sex with men" (MSM; Chow et al., 2019). Another approach focuses solely on the basis of *genital arousal*: are a person's genitals aroused by males, females, or both? This is a measure some researchers have argued to be more straightforward in males but is methodologically and analytically more complex to interpret among females (Bailey, 2009). For people who study how people interpret their own *identities* and experiences, it is essential to focus on the connections between behaviors, identities, and attractions, as the identity develops (Cass, 1984; Katz-Wise et al., 2017).

A common approach is to focus on *attraction* as the key element of sexual orientation. This approach separately assesses the degree of attraction to the female sex (*gynephilia)* and the degree of attraction to the male sex (*androphilia).* People who are *androphilic* are attracted to males, those who are *gynephilic* are attracted to females, and *ambiphilic* people are attracted to both (Dawson et al., 2017). A person can be high or low on both dimensions separately. Heterosexuals are high in one dimension and low in the other, *asexuals* are low in both, and there are many possible combinations of low, medium, and high gynephilic and androphilic attractions that are possible. An "androphilic male" would be socially labeled as a "gay male," at least in Western cultures. This approach, however, does not cover all potential attractions. For example, some biological males are attracted to people who have male genitalia but who also identify as a woman, have feminized their appearance through hairstyle and clothing choices, surgically modified facial features, and altered breast size through hormones or surgical modification. Attractions to these transgender women—sometimes termed "gynandromorphophilia" (Rosenthal et al., 2017)—are not readily captured in the traditional gynephilia/androphilia framework, nor are attractions to intersex people.

To fully understand the breadth of sexual orientation and mating strategies, we often need to understand more than just one facet of sexual orientation at a time. Diamond (2003) emphasizes the importance of separating out sexual versus romantic orientation: who we find sexually attractive can differ from the people we feel romantic attractions for. Peplau (2001) further highlights that

attraction can develop to a given person over time and might not be strictly based on biological sex. Therefore, rather than focusing our attention on just one dimension such as genital arousal, we can broaden our focus to measure multiple dimensions of sexual orientation and sexuality simultaneously. Sexual configurations theory focuses on the complexity of orientations and attempts to draw together many different dimensions simultaneously, such as attraction to different genders and sexes, degree of openness to having multiple partners, and desires for nurturance (van Anders, 2015).

In practice, however, many researchers have tried to capture the complexity of orientation along just one continuum: the Kinsey scale (Kinsey et al., 1948). This scale allows for more nuance than three categories (heterosexual, homosexual, bisexual) by asking people to indicate their sexual orientation along a 7-point continuum from exclusively homosexual to exclusively heterosexual. This scale allows for some more nuance for people who report attractions across multiple sexes and genders, and they can incorporate their own label into this single continuum based on their compilation of behaviors, attractions, and fantasies (Galupo et al., 2014).

While the Kinsey scale allows more flexibility than a three-category system, it is missing many elements, including the element of *sexual fluidity* (*erotic plasticity*) over time. People's sexual orientations can change across their lifetime or even on a day-to-day basis. Many studies suggest that female sexuality is more fluid than male sexuality (Baumeister, 2000), including less stability in day-to-day sexual attractions (Diamond et al., 2017), although some research finds only small differences (Katz-Wise & Hyde, 2015). This fluidity across time, and multiple dimensions of sexual orientation, is captured through measures such as the Klein Sexual Orientation Grid (Klein, 1993).

Defining Gender

In addition to considering variations in sex and sexual orientation, it is important to further consider gender as well. Much of the existing research on mate preferences does not discriminate between sex and *gender identity* (a person's internal, deeply held sense of their identity). People who are *transgender* have a gender identity or gender expression that differs from what is historically or conventionally associated with the sex they have assigned at birth (GLAAD, 2020). This contrasts with someone who is *cisgender*, whose assigned sex matches their gender identity. While it is important to acknowledge this distinction as well as consider those individuals who are not represented by this binary, the correlation between sex and gender has been extremely high in many

previous studies (Gates, 2011), suggesting the likelihood of strong evolutionary selection on these traits. To use the metaphor supplied by Schmitt (2016), there are many elements to sex and gender, which can act as interconnected, dimensional dials that often turn in one direction but can also turn independently, creating diverse identities and attractions. Given that sex and other-sex attraction is the engine that drives evolution, many of these dials will often covary systematically with each other (e.g., most people with XY chromosomes also have a male-typical gender identity and attraction to women), but in other people these dials turn separately from each other.

These variations raise the question of how we should define sexual orientation when standard labels rely on the binaries of male and female, which do not always match a person's gender identity. One strategy for improving mating research is to include a series of questions related to gender, sex, and sexual orientation, so that these many different variations can be assessed (Bauer et al., 2017). This will help us more fully understand the variations in mating strategies across people with a wide variety of sex-gender-sexual orientation configurations. Many researchers also advocate for using a multi-item assessment of sex/gender that captures sex assigned at birth and gender identify (e.g., Haupert et al., 2019).

Prevalence of Different Sexual Orientations

An examination of current industrialized and nonindustrialized countries, along with historical records, highlights just how prevalent various sexual orientations are worldwide, including distinctions between same-sex sexual behaviors, attractions, and identities. This prevalence highlights the importance of understanding this variation in sexual orientation and the mating patterns tied to these orientations.

Prevalence across Industrialized Nations

A review of US national studies estimated that approximately 3.4 percent of women and 3.6 percent of men identity as bisexual or lesbian/gay (Gates, 2011). When we break that down further, we see that women were more likely to identify as bisexual (2.2 percent) compared to lesbian (1.1 percent), whereas men were less likely to identify as bisexual (1.4 percent) compared to gay (2.2 percent). People in younger generations are identifying as *LGBTQ* (lesbian, gay, bisexual, transgender, queer) at higher rates: 7.3 percent of millenials born 1980–1998 reported this identity (Gates, 2017), and 13.8 percent of female youth and

7.0 percent of male youth identified as not heterosexual (Phillips et al., 2019).

Looking outside of the United States, a study hosted by the British Broadcasting Company measured sexual identity and sexual attraction in 28 nations (Rahman et al., 2020). The nations were primarily in Europe, followed by Asia and North America. Across the countries, the most common *sexual identity* was straight (85–96 percent), followed by bisexual (4 percent-11 percent) and gay/lesbian (1 percent-11 percent). More women than men identified as bisexual. *Sexual attraction* showed even more variability. Men were more likely than women to identify as only being attracted to the opposite sex (83 percent vs. 66 percent), whereas women were much more likely to be moderately attracted to the same sex (27 percent vs. 10 percent), with equal proportions of men and women reporting bisexual attractions (7 percent respectively). In a study of secondary students in Hong Kong, a minority of girls and boys reported being homosexual (1.5 percent vs. 2.6 percent), bisexual (1.8 percent vs. 3.7 percent), or unsure of their sexual orientation (10.7 percent vs. 8.8 percent) (Zhang et al., 2017).

Prevalence across Nonindustrialized Societies

There are many documented examples of same-sex sexuality across cultures and throughout history, and this is true for Africa, Europe, Oceania, Asia, and the Americas. A classic example is Hoffman's (1980) analysis of Greek social structures and culture. Hoffman (1980) states that though most men married, and few engaged in exclusively homosexual relationships, homosexual behavior was widely spread throughout all social classes. Similarly, the Tokugawa period of Japan (1600s-1800s) was when *nanshoku* arose: the practice of accepting male-male love and exclusive preference for male partners (Leupp, 1997).

The many examples of same sex sexuality across cultures are reviewed in more detail by Kirkpatrick (2000). He notes that there is tremendous variation across these cultures. For example, behaviors are highly variable in terms of frequency (from very limited to nearly universal), in terms of sexes and genders who engage in the behavior (men, women, transgender), and in terms of the ages of those involved (juveniles, adults, or mixed ages) (see also Rupp, 2001).

While many cultures had instances of same sex behavior across history, the prevalence and level of acceptance have varied substantially. Looking at South America, one commonly cited example is the Nicaraguan concept of engaging in penetrative sex with a "cochón"—an effeminate man who is receptive to anal sex. Although being the receptive sexual partner is stigmatized, being the penetrative partner is not (Lancaster, 1988). A similar pattern has been observed

in fishing villages in southern Brazil. Specifically, Cardoso (2005) found that there was a subset of men in the fishing village that primarily had sex with women but would have penetrative sex with a man on occasion. However, they were never the one who was receiving.

Variations across Ecological and Cultural Factors

Acceptance and prevalence of same-sex sexual relationships varies according to ecological, economic, cultural, and population factors. Below we provide two examples: Lesotho and China. One example of this is the mummy-baby relationships in Lesotho, a country in southern Africa (Gay, 1986). In this society, nearly half of the men migrate to South Africa, primarily in search of work. In the field site described in this study, 82 percent of the men were working away from the village for either all or part of 1997. This created a dramatically skewed sex ratio in the population, leaving many adolescents and young women without cross-sex partners available. In these mummy-baby relationships, typically a relatively older woman will pair with a relatively younger woman. These relationships typically include emotional intimacy, gift giving, hugging, and kissing. Less well understood is the extent to which these couples engage in genital activity because this behavior was considered to be more taboo. The researcher did, however, report that multiple interviewees confirmed that some relationships include sexual behavior along with sensual intimacy. Many of these women form cross-sex marriages as adults which reflects what we now know about sexual fluidity in women and the ability for orientation to fluctuate across time and circumstance (Diamond, 2008).

Mainstream media in China often frames homosexuality negatively (Chang & Ren, 2017), and the majority still believe homosexuality is always wrong. This is, in part, due to Confucian values that emphasize the importance of family, such that purpose of sex is to procreate and form a family (Xie & Peng, 2018). These shifts are interesting because Chinese historians note how attitudes have shifted across time, as same-sex sexual behaviors often being acceptable prior to extensive contact with Western cultures and the Communist revolution. Some researchers credit the one-child policy for helping to indirectly accelerate a return to increased acceptance of same-sex sexual behavior, by refocusing the function of sexual activity away from reproduction and towards pleasure (Zheng, 2014). High levels of stigma in some cultures, and across generations within a culture, may depress the ability of people to develop same-sex attractions or engage in same-sex sexual behaviors.

Sexual Orientation Similarities and Differences in Sociosexuality

The fact that same-sex behaviors are prevalent across species and cultures highlights the importance of understanding the mating behaviors and preferences of all sexual orientations, and not just those that are traditionally accepted and promoted, such as heterosexuality. Here we first examine the associations of sexual orientation to one of the most well-researched facets of mating strategies: *sociosexuality* (Simpson & Gangestad, 1991). People with a *restricted sociosexual orientation* prefer being emotionally close with a partner before engaging in sex and rarely engage in casual sex. In contrast, people with an unrestricted sociosexual orientation are comfortable with sex without emotional connection or commitment, and are more likely to have casual sex. Sociosexuality includes *behaviors* (e.g., number of one-night stands and sex partners), *attitudes* (e.g., reported comfort having sex without commitment), and *desires*/*fantasies* (e.g., frequency of fantasies and spontaneous sexual arousal for people they are not in a relationship with) (Simpson & Gangestad, 1991). More recent scales assessed these different aspects of sociosexuality through separate subscales (Penke & Asendorpf, 2008).

One intriguing question evolutionary psychologists ask is whether men and women differ, on average, in sociosexuality. This research has often been motivated by *parental investment theory* (Trivers, 1972), and psychological perspectives that build up on it, such as *sexual strategies theory* (Buss & Schmitt, 1993) and *strategic pluralism theory* (Gangestad & Simpson, 2000). Parental investment theory notes that, in many species, there are key differences between males and females in the costs of reproduction. Females generally have higher *minimum obligatory biological costs* associated with reproduction than males do: females must allocate substantial energy and calories to pregnancy and breast feeding, whereas the minimum obligatory costs for males is relatively lower (cost of producing sperm and the energy expended in the mating bout). Furthermore, females typically have *lower reproductive potential* than males: in humans, most women will have a maximum potential number of offspring between ten and twenty, whereas for men the maximum potential is in the thousands.

Parental investment theory proposes that the different minimum costs and maximum potential offspring will impact the mating strategies of each sex. This theory proposes that males will be *relatively more open* to sexual encounters with a wider variety of individuals in a wider variety of contexts. In contrast, it expects that females will be *relatively less open* to sexual encounters, and with a narrower set of individuals in a narrow set of contexts. This is often referred to

as females being *choosier* than males when selecting mates.

We emphasize the "relative" nature of these comparisons. The theory can easily be misunderstood as indicating that "men are short-term oriented, and women are long-term oriented," which is not the case. Both males and females, of many species, engage in short-term and long-term mating. Furthermore, the *actual costs* of mating are typically different from the *minimum costs* of mating. For example, if females are choosier than males, this increases pressure on males to provide resources, engage in intrasexual competition, and to develop metabolically expensive traits that are preferred by females. These all raise the costs of mating to males, which may then impact their mating strategies (Frederick et al., 2013).

In addition to notable variations across sexes in mate preferences, there is much variation within each sex as well (Simpson & Gangestad, 1991). Building on parental investment theory, *sexual strategies theory* emphasizes that men and women have a menu of short-term and long-term mating strategies that they employ depending on the context (Buss & Schmitt, 1993), and *strategic pluralism theory* highlights how strategies vary depending on one's own traits, such as physical attractiveness (Gangestad & Simpson, 2000). Sex is just one of thousands of factors that can impact any given person's mating strategy, albeit an important one. Research has generally found notable differences between men and women in sociosexuality (Lippa, 2009; Schmitt et al., 2012).

Sexual Orientation Differences in Sociosexuality among Men

Overall, the existing research suggests that men who have sex with men are fairly similar to heterosexual men in sociosexual attitudes and desires, but exhibit much more unrestricted sociosexual behaviors than do heterosexual men.

There were no differences between gay, heterosexual, and bisexual men in sociosexual attitudes in cross-cultural study of forty-nine nations (Schmitt et al., 2007). This is consistent with other research finding no differences in unrestricted attitudes between gay and heterosexual men (Bailey et al., 1994; Howard & Perilloux, 2017; Waldis et al., 2020a). Some research has found no differences in sociosexual desire (Howard & Perilloux, 2017), whereas other studies have found that gay men report slightly greater sociosexual desire (Waldis et al., 2020a).

An interesting finding is that even though sociosexual attitudes and behaviors are similar among men of different sexual orientations, their sexual behaviors are notably different. Across many studies, sexual minority men report more lifetime sex partners and casual sex partners than heterosexual men did (Bőthe et al.,

2018; Vrangalova & Savin-Williams, 2012), and more unrestricted sociosexual behavior (Schmitt, 2007; Waldis et al., 2020a). For example, a British national study found that more gay men than heterosexual men reported ten or more lifetime sexual partners (71 percent vs. 37 percent percent) (Mercer et al., 2016). Studies in the United States found that the median number of lifetime sex partners was higher for gay men than heterosexual men (fifteen vs. four) (Glick et al., 2012). This greater number of sex partners among bisexual and gay males than heterosexual males is found among adolescents (Poteat et al., 2019), as well as adults (Jeffries, 2011).

In contrast to pursuing a short-term or long-term mating strategy, some people pursue a *pluralistic mating strategy*—they pursue multiple short term and long-term partners simultaneously. One common way this is achieved is through having one long-term partner and committing infidelity with other partners. Another approach to a pluralistic mating strategy is to agree with partner(s) to be in a non-monogamous relationship (Mogiliski et al., 2015). Consensually nonmonogamous relationships can be defined as "any relationship arrangement in which the partners agree to have extradyadic sexual or romantic relationships" (Conley et al., 2013, p. 2). There are different ways of conceptualizing different types of consensual nonmonogamy, but three subtypes include *polyamory* (romantic, loving, and long-term in nature); *swinging* (sex with people other than partner), and *open relationships* (primarily sexual, but can also be romantic) (Haupert et al., 2017). In national studies, sexual minority men are also more likely to have had consensually non-monogamous relationships than heterosexual men, with about one third of gay men reporting these relationships (Haupert et al., 2017).

The findings indicate a clear pattern—sexual minority men are more likely than heterosexual men to have unrestricted sociosexuality in the behavioral sense, despite the fact that their sociosexual attitudes are similar. Why might this be? There are several possible interpretations of these findings. The first falls in line with theories derived from parental investment theory. If men evolved a predisposition to be relatively more open than women to sex with a wider variety of partners in a wider variety of contexts, then people seeking male partners will be better able to find a willing casual sex partners. As Symons (1979) proposed, the primary factor constraining heterosexual men from having more short-term sexual partners is that they are seeking these encounters with the sex that is choosier about who they have short-term sex with (female partners) than the ones sought by gay males who are more accepting of short-term mating (male partners).

We noted earlier that it can be easy for some people to misinterpret the

implications of parental investment theory and to think categorically (men are short term, women are long term), and therefore caution against the same categorical mistake when thinking about gay/bisexual versus heterosexual men. There is substantial variation among gay/bisexual men in sociosexuality, just as there is among heterosexual men and women. One finding we draw attention to is that the mean number of sex partners is substantially higher among gay men than the median number of sex partners. This is due to the fact that a subset of gay men have highly unrestricted sociosexuality and many partners, whereas a substantial number of gay men do not. One of the first large-scale national studies of gay men found that 71 percent of gay men said they preferred long-term monogamous relationships to other arrangements (Lever, 1994). In the study, more than half (52 percent) said they were monogamous in their current or most recent relationship, while another 28 percent were supposed to be monogamous but one or both partners cheated. Only 20 percent stated that they were in open relationships. More recent studies identify a roughly 33 percent prevalence of current or past consensual nonmonogamy, meaning that 67 percent have not had these relationships (Haupert et al., 2017). Looking at people in romantic relationships, many of the experiences are similar among sexual minority and heterosexual men (Peplau & Fingerhut, 2007). Therefore, although parental investment theory and the perspectives derived from it offer an initial useful understanding of sexual orientation differences in sociosexuality, there are additional factors that need to be considered.

Many additional factors contribute to the variations in sociosexual behavior among gay men. First, gay marriage was illegal for centuries in the United States and highly stigmatized. There is a risk of severe social stigma, loss of job, and discrimination for those openly identifying as gay. These social pressures can funnel some gay men to favor discreet encounters rather than risking the dangers brought on by having socially visible long-term relationships. Furthermore, all men are exposed to socialization that celebrates male sexual prowess as part of masculinity, which can further shape men's willingness to pursue casual sex. The multiple routes through which gay men develop greater unrestricted sociosexual behaviors despite similar sociosexual attitudes, and identifying how evolved predispositions interact with environmental inputs, is worth further exploration.

Sociosexual Attitudes, Desires, and Behavior among Women

Overall, the existing research points to lesbian women being similar or slightly less restricted in sociosexuality than heterosexual women (Howard & Perilloux, 2017; Lyons et al., 2014; Schmitt, 2007; Waldis et al., 2020b). In

contrast, bisexual women are notably less restricted than lesbian and heterosexual women in attitudes and behaviors (Schmitt, 2007; Semenyna et al., 2018; Vrangalova & Savin-Williams, 2012). These patterns can be observed even in adolescence. Bisexual females were more likely to have had sex with an unfamiliar partner (51 percent) than lesbian females who only have sex with women (30 percent) and heterosexual females who only have sex with men (20 percent) (Poteat et al., 2019). One important source of variation in sexual behavior may be self-described masculinity and femininity. Sexual minority women who described themselves as "feminine" or "androgynous" reported more male sex partners than "masculine" women, but masculine women reported more female sex partners (Lindley et al., 2007).

Two recent national studies found that heterosexual women were less likely to have ever been in a consensually nonmonogamous relationship than bisexual and lesbian women (Haupert et al., 2017). In terms of attitudes, sexual minority women were more willing to consider these relationships than heterosexual women were (Moors et al., 2014).

The similarities between lesbian and heterosexual women are interesting because the potential obligatory biological costs of mating with another female are notably lower than the costs of mating with a male. Similar to the proposals for gay men, one interpretation of these findings is that evolved, environmental, and cultural factors converge to reduce women's interest in pursuing casual sex.

The patterns for bisexual women, however, diverge notably from the patterns of other women. For instance, bisexual women tend to have more sexual partners than heterosexual women. Mark et al. (2014) found that bisexual women were more likely than lesbian and bisexual women to feel that being monogamous was a sacrifice on their part. One speculation for the higher sociosexuality among bisexual women is that they have a stronger spontaneous sexual arousal than do other groups of women. One study found that bisexual women were higher than other women in *sexual sensation-seeking* (e.g., enjoying new and exciting sexual experiences) and *sexual excitability* (e.g., becoming aroused easily when touched by an attractive stranger) (Stief et al., 2014). Some have supported this with research finding evidence of higher sex drive among bisexuals as measured through two items in a large internet sample (I have a strong sex drive; It doesn't take much to get me sexually excited; Lippa, 2007) and in a sample of Canadian college women who completed a validated four-item measure of sex drive (Semenyna et al., 2018). This suggests that a larger subset of bisexual women may have high sex drives relative to other women, which would may relate to greater sexual sensation-seeking and excitability, leading to more unrestricted sexual behaviors. We always must be cautious to

remember, however, that sex and sexual orientation differences are not categorical, there is important variation within groups and overlapping distributions across groups.

Preferences for Physical Traits in Mates

The existing literature on self-reported mate preferences among sexual minorities is scant in most areas, with a few exceptions. In this section, we review some of the major studies and findings from Western industrialized cultures, focusing on the findings for different traits and using different methods (e.g., personal ads and self-reported preferences).

The Importance of Physical Attraction

Physical attraction is important to many people when selecting a long-term partner (Buss, 1989; Fales et al., 2015). In a cross-national study, men ranked "good looks" as the second most important trait in a partner and "face attractiveness" as the fifth most important (Lippa, 2007). In contrast, women ranked good looks eighth and facial attractiveness ninth. None of the comparisons between sexual orientation within each sex exceeded $d = |0.10|$. Overall, these findings suggest that many men and women, regardless of sexual orientation, value physical attractiveness, but that men in particular value looks in a long-term partner.

Preferences for Sexual Dimorphic Traits

Although there is extensive research on the importance of good looks and the physical traits preferred by men and women, there have been few systematic comparisons across different sexual orientations. The research on preferences for female physical traits have often focused on traits potentially linked to cues of age, fertility, estrogen levels, and health. Research on preferences for male traits have also included physical traits linked to dominance, testosterone, and formidability. We examine how sexual orientation relates to preferences for *sexually dimorphic* traits—those that differ notably on average between males and females—such as muscularity, height, body fat, voice, breasts, and face.

MUSCULARITY AND MASCULINITY

One notable difference between male and female body types is that men have broader shoulders and greater upper body and grip strength. Many women express preferences for men with moderately muscular and toned bodies

(Frederick & Haselton, 2007; Gray & Frederick, 2012). This research has generally emphasized the benefits of selecting a mate who is physically formidable (Snyder et al., 2011), as well as potential benefits from mating with a male who might pass predispositions for a robust body onto offspring (Frederick & Haselton, 2007). Furthermore, muscularity is held up as socially prestigious, which encourages men to desire muscularity in themselves and women to desire muscularity in their male partners (Frederick et al., 2005).

Many gay men also report this preference for masculinized body types (Lanzieri & Hildebrandt, 2011). For instance, Howard et al. (1987) analyzed mate preferences among heterosexual couples, same-sex male couples, and same-sex female couples. Gay men and lesbian women were more likely than their heterosexual counterparts to prefer athletic and muscular partners. Several studies also show that gay men tend to prefer men with lean, muscular, or athletic bodies and relatively broad chests (Bartholome et al., 2000; Hatala & Predhodka, 1996; Swami & Tovée, 2008; Varangis et al., 2012). In online personal ads, gay men will often mention their fitness level or gym interest and include shirtless photos to draw attention to their physiques (Miller, 2015).

Additional factors may shape these pressures. For example, femininity among men is often stigmatized and gay men are often stereotyped as being feminine. Some gay men combat this stigma by enhancing their own muscularity and select a partner who is relatively masculine, including in muscularity, because these men are more socially accepted (Miller, 2015). In fact, gay men often report a preference for men with masculine body types and personality traits in personal ads, whereas lesbian women often express preferences for sex-typical or feminine characteristics (Bailey et al., 1997).

The above research generally suggests that gay men prefer lean and muscular men, but there are stereotyped subtypes of gay men with different preferences. For example, some men prefer “twinks” who are slender with minimal muscle bulk and often appear young. Others prefer “muscle boys” who tend to be more athletic, whereas others prefer “bears” who tend to have greater body mass (Moskowitz et al., 2013).

Gay men (much like androphilic women) could derive *direct benefits* from mating with muscular men, such as those that come along with a partner who is physically formidable, especially when this muscularity enhances their status, prestige, and abilities to engage in intrasexual competition.

BODY FAT LEVEL AND WAIST-TO-HIP RATIO

Preferences for women’s body fat levels vary dramatically across cultures and historical contexts. In a cross-national study of forty-one sites across twenty-six

countries, relatively slender women were preferred in the industrialized countries (Swami et al., 2010). In rural populations in Malaysia and South Africa, however, relatively heavy women were preferred. These results are similar to research finding preferences for heavier women in Ghana versus relatively thinner women in Ukraine and United States (Frederick et al., 2008). In resource-poor environments, high body fat level may be a cue to health and access to resources, whereas in resource-rich environments, low body fat may be a cue to these traits as well as youth and *nulliparity* (never having been pregnant) (Gallup & Frederick, 2010).

The existing research finds small differences between heterosexual and lesbian women in their preferences surrounding body weight. Swami and Tovée (2006) found a small difference between lesbian and heterosexual women, with heterosexual women rating women with a body mass index (BMI) of 21 most attractive compared to a BMI of 23 among lesbian women. Similarly, a study presenting eight hand-drawn images of women that varied in apparent body fat, waist-to-hip ratios, and breast sizes also found similar preferences between heterosexual and lesbian women (Cohen & Tannenbaum, 2001). In samples taken from Brazil and the Czech Republic, heterosexual men and sexual minority women both preferred women with relatively large buttocks, medium to large breasts that had a youthful or "perky" appearance, and a waist-to-hip ratio of 0.70 (Valentova et al., 2017).

Overall, the findings indicate that many people attracted to women tend to prefer partners with some exaggerated feminized physical traits. It is important to note, however, that variation across cultures, individuals, and time has not systematically been studied.

PREFERENCES FOR FACES

Most existing research finds that gay men prefer relatively masculinized male faces such as those with lower and more prominent brow ridges, wider jaws, and larger chins (Cassar et al., 2020; Glassenberg et al., 2010; Shiramizu et al., 2020) or are roughly equally likely to prefer feminized male faces and masculinized male faces (Welling et al., 2013). One study, however, found that gay men who described themselves as more masculine preferred relatively more feminine male faces (Valentova et al., 2013). Gay men were also more likely to prefer facial hair (and body hair) than heterosexual women (Valentova et al., 2016).

When asked to choose between a series of masculinized and feminized female faces, lesbian women preferred the feminized faces the vast majority of the time (Welling et al., 2013). Among self-identified heterosexual women, the heterosexual women who reported more attraction to women had stronger

preferences for feminine male faces and women who reported more attraction to men had stronger preferences for masculinized faces, highlighting the importance of considering sexual orientation variations within the crude label of "heterosexual" (Batres et al., 2020).

PREFERENCES FOR HEIGHT

A great deal of research finds that women tend to prefer male partners who are relatively taller than themselves, men tend to prefer relatively shorter partners, and preferences for height are related to a person's own height (Salska et al., 2008). A study of Australian sexual minority men found that their ideal partner was on average 5′11″, and that taller men preferred tall partners (Griffiths et al., 2017). In a study of Brazilian and Czech participants, Valentova et al. (2014) found that the most popular preference among sexual minority men and women was preferring a taller partner, with the remainder preferring someone their own height or shorter. These preferences, however, varied by sexual role. Men who preferred to be dominant in their relationships and sexual activities preferred shorter partners, whereas men who preferred to be submissive preferred taller partners (Valentova et al., 2014).

PREFERENCES FOR VOICE

Voices are highly sexually dimorphic—there is minimal overlap in the fundamental frequency (voice pitch) between males and females (Hollien et al., 1994). Valentova et al. (2013) found that both heterosexual women and gay men preferred male voices that were relatively more masculinized with deeper pitch.

Age Preferences

There has been substantial research on age preferences and preferences for cues of youth in heterosexual men and women (Conroy-Beam & Buss, 2019). This research is often motivated, in part, because evolutionary psychologists have long theorized that there are sex differences in preferences for youth in a partner, primarily because youth is more strongly linked to fertility and future reproductive potential for women than for men. Older age in men, in contrast, is often linked to status and resources. Consistent with these proposals, heterosexual men often express a preference for relatively younger partners, whereas heterosexual women often express a preference for relatively older partners (Kenrick et al., 1995). These preferences vary notably depending on the type of relationship. For example, older men prefer someone relatively close in age to them for a marriage partner but notably younger than themselves for a

casual sex partner or in a sexual fantasy (Buunk et al., 2001).

In a cross-national survey, men ranked age as the tenth most important trait in a partner (out of twenty-three traits) and women rated it the eleventh most important. There were no differences between lesbian and heterosexual women, and gay men ranked age slightly higher than did heterosexual men (Lippa, 2007). Studies have consistently found that older gay men often prefer a partner who is younger than themselves, with some men also preferring those who are the same age as them (e.g., Rasmussen et al., 1998). Further research shows that there is variability in age preferences in those who identify as more masculine rather than feminine, with masculine gay men preferring younger partners and feminine men preferring older partners (Burrows, 2013).

Preferences for Status and Other Traits

In a cross-national study, participants ranked the importance of twenty-three different traits when choosing a long-term partner (Lippa, 2007). There were no large differences between heterosexual and gay men, or between heterosexual and lesbian women. In fact, all but one of the effect sizes in these comparisons were smaller than $d = |0.20|$, indicating a high degree of overlap in preferences. For example, the mean rankings of ambition, industriousness, status, and money were nearly identical between heterosexual and gay men (d's = |0.00 to 0.09|). Similarly, all differences between heterosexual and lesbian women were nonsignificant or small (d's = |0.02 to 0.11|). These findings suggest that sexual orientation is not strongly related to mate preferences for status in a partner, but it is important to note that more notable variations between cultures and ecologies would likely impact these preferences (Pillsworth, 2008).

Tops, Bottoms, Versatiles, Butches, and Femmes

Some sexual minority men and women differ in their preferences for roles during sex, and these preferences can dictate the types of partners they seek. This is particularly pronounced variation among gay men regarding their preferences to receive penetration or not. *Tops* refers to people prefer the insertive position during sex, *bottoms* who prefer receptive roles, and *versatiles* who prefer both. In a Chinese study, tops described themselves has having more masculine traits and bottoms described themselves as having more feminine traits (Zheng et al., 2012). It is likely that a bottom will only seek out relationships with a top or a versatile and a top will generally seek bottoms or versatiles.

Another way of examining variability of mate preferences within sexual

minority groups is to examine differences in men and women across *butch* (masculine traits or appearance), *femme* (feminine traits or appearance), and *androgynous* (relatively equally masculine and feminine) identities. This butch versus femme distinction has been identified as sources of variability in mate preferences in multiple cultures (Levitt & Horne, 2002; Zheng & Zheng, 2013). These identity labels may further be connected to childhood or current gender nonconformity, which in turn has implications for mate preferences. *Gender nonconformity* refers to when a person does not conform to the typical social behaviors or psychological traits that are typical for their sex in their society. For example, it might include preferring clothing, toys, and playmates of the other sex; identifying with other-sex characters in media; or desiring to be a member of the other sex (Rieger et al., 2008). Studies have found that gender nonconformity is often linked to sexual orientation (Bailey & Zucker, 1995; Rieger et al., 2008), and also to identification as butch or femme (Zheng & Zheng, 2016).

These identities and sexual roles factor into mate selection for sexual minority men and women. People often seek partners whose sexual role preference is compatible to their own (Bailey et al., 1997; Moskowitz & Roloff, 2017). When couples have complementary sexual roles, this increases the likelihood of sexual satisfaction in relationships (Moskowitz & Garcia, 2019).

Evolutionary Theories

An evolutionary understanding of sexual orientation and preferences has continued to intrigue evolutionary scientists, with a variety of considerations for the ultimate etiology of same-sex sexual attractions. It is relatively easy to imagine how some degree of same-sex sexual behaviors could be adaptive. For example, they could foster stronger alliances and bonds among individuals of the same-sex, serve as practice for developing sexual skills, and encourage cooperation and allocare of offspring. They could also emerge as a by-product of natural variation in sexual arousal (for reviews, see Bailey et al., 2016; Bailey & Zuk, 2009; Bartova & Valentova, 2012; Jeffrey et al., 2018; Safron, 2018; Savolainen & Hodgson, 2017; Valentova & Varella, 2016). What has been especially challenging is understanding the evolution of exclusive same-sex attraction and behavior—how would genes that sharply inhibit reproductive behavior be passed on to future generations and remain in the population?

It is clear from the research on human and nonhuman animals that bisexual and exclusively same-sex attractions exist reliably in populations. In the next subsections, we present some of the key proposals that explain how evolutionary

processes can lead to same-sex sexual attraction. Our focus here is not on the proximate biological mechanisms—such as genes and hormones—that correlate with sexual orientation (e.g., Balthazart, 2020; Bogaert & Skorska, 2020; Wang et al., 2019). Additionally, our focus is not on a systematic evaluation of which evolutionary theories are best supported by the evidence. Rather, we highlight a few examples of proposals by evolutionary biologists and psychologists regarding the potential routes through which same-sex sexuality could emerge in humans. Most evolutionary proposals fall into two general categories: adaptive explanations and by-product explanations.

Adaptive Explanations

Adaptations are traits that emerged through natural selection because they directly or indirectly facilitated reproduction during the period in which it evolved (Buss et al., 1998). Adaptationist explanations focus on how exclusive same-sex sexual attraction or behaviors could ultimately increase the *inclusive fitness* of an individual.

KIN SELECTION THEORY

Kin selection theory (Wilson, 1975) proposes that homosexuality could have been evolutionarily advantageous (or neutral) if the benefits conferred to extended family members, such as nieces and nephews, outweigh the negative reproductive costs of not mating with members of the other sex. This would enable genes predisposing people toward homosexuality to remain in the population. Studies in Samoa and Java (Indonesia) have found evidence consistent with the theory. In Java, androphilic males gave 169 percent more in resources to nieces and nephews than did gynephilic men. Although this is consistent with the theory, the additional support to relatives by androphilic males only accounted for 20 percent of the reproductive costs associated with androphilia (Nila et al., 2018). In Samoa, the *fa'afafine*—a term that translates to "in the manner of a woman" and describes third-gender androphilic males who are widely accepted in the culture—gave significantly more to nieces and nephews than heterosexual men and women (VanderLaan & Vasey, 2012; Vasey & VanderLaan, 2010). Research has also shown that the presence of *fa'afafine* in family units is associated with elevated reproduction among extended relatives in both the maternal and paternal line, possibly due to additional support and allocare provided by these nonreproducing family members (VanderLaan et al, 2012).

However, not all research has supported this hypothesis, including studies in

the United States, United Kingdom, and Japan that did not find supporting evidence (Bobrow & Bailey, 2001; Rahman & Hull, 2005; Vasey & VanderLaan, 2011). These findings raise the question as to whether the theory is supported, and whether or not the applicability of theory depends on how accepted and integrated these androphilic men are in the population (Vasey et al., 2020).

AFFILIATIONS, ALLIANCE, AND ALLOPARENTING

Other researchers have focused on how homoerotic behavior could lead to increased access to resources and opposite-sex mating opportunities through the formation and maintenance of social bonds (Muscarella, 2000; Muscarella et al., 2005). Same-sex sexuality that promotes bonds and alliances could lead to elevated social standings and additional resources. More generally, same-sex sexual attraction and behavior are related to traits that help humans thrive in social, affiliative environments, namely, through reduced aggression, increased communication, and improvement of social integration (Barron & Hare, 2020).

Relatedly, female sexual fluidity could facilitate the formation of same-sex pair-bonds among women. Female *alloparenting*, or shared care of genetically unrelated offspring, could benefit women, especially when males abandon the relationship, die, or are not physically present for long periods of time (Kuhle & Radtke, 2013). In terms of polygyny, homoerotic behavior among cowives would decrease tension and conflict among the family, thus securing communal upbringing of all offspring (Kanazawa, 2017). Contrary to this proposal, however, cross-cultural evidence from sixty-nine societies suggests cowives tend to prefer "respectful distance," recognizing competition for access to their shared husband (Jankowiak et al., 2005).

By-product Theories

In contrast to adaptations, by-products emerge as a side effect of adaptations being formed (Buss et al., 1998). For example, a by-product of big brains is that we are able to read this text, even though that was clearly not the reasons that big brains evolved initially. Some people have explored whether same-sex sexual behavior and attractions emerge as a by-product of other adaptations.

FECUNDITY

If the genes that predispose individuals to nonheterosexuality confer reproductive advantages on heterosexual relatives with the same genes, then these genes can be maintained in the population. Imagine this scenario: a version of a gene on the X chromosome causes some women to be very fertile and to

survive childbirth at high rates. When this gene becomes activated in males, it sometimes triggers exclusive same-sex behavior. This gene could easily be maintained in the population because androphilic males would have female relatives with high reproductive success.

One version of this proposal, the *sexually antagonistic gene hypothesis*, suggests that when gene(s) are present in one sex, they can cause or contribute to nonheterosexuality in the other sex (Camperio Ciani et al., 2004; VanderLaan & Vasey, 2011). Researchers exploring this hypothesis have primarily focused on how male nonheterosexuality is related to the fecundity of the males' female relatives along the maternal line. For example, female maternal relatives of androphilic males in Italy, Independent Samoa, and the Istmo Zapotec (Southern Mexico) have been documented as having higher rates of reproduction than those female maternal relatives of heterosexual men (Camperio Ciani et al., 2004; Semenyna et al., 2017) and the same was true in the maternal line of bisexual Italian men (Camperio Ciani et al., 2009). Other research, however, has not supported this theory (Blanchard, 2012).

The second version of this proposal, the *overdominance hypothesis*, suggests that genes predisposing people to nonheterosexuality may be heritable and subject to recombination. When in the homozygous form, this gene causes nonheterosexuality. Yet, when in the heterozygous form, it increases a heterosexual individual's fecundity, theoretically enough to offset the nonheterosexual individual's lower level of reproduction. One version of the overdominance hypothesis suggests that nonheterosexuality would be associated with gender-atypical traits. When these gender-atypical traits are present in heterosexual individuals, it increases their fecundity, which leads to the preservation of those genes in the gene pool (Zietsch et al., 2008). Utilizing a large study of twins, gender atypicality was associated with homosexuality (Zietsch et al., 2008). Yet, when gender atypicality was present in heterosexual individuals, it was associated with having more sex partners. In addition, the heterosexual twins of nonheterosexual individuals had more sex partners than heterosexual twins with a heterosexual sibling.

LIFE HISTORY THEORY

Life history theory (LHT) is an evolutionary perspective detailing the power of early experiences to shape development and later life outcomes (Ellis et al., 2009). For example, early life adversity such as abuse, neglect, and changes to the family could have downstream effects on how organisms allocate their limited resources and energy in order to enhance survival and reproduction in a particular environment (Brumbach et al., 2009; Belsky et al., 2012; Del Giudice

et al., 2016). Early life experiences can catalyze facultative shifts in individual's resource allocation to either growth and development or mating effort (Ellis et al., 2009; Frankenhuis et al., 2016).

Life history strategies are generally conceptualized as *fast* and *slow* (Belsky et al., 2012). Stable and predictable developmental environments push individuals toward a slower life history strategy (Del Giudice et al., 2016) involving long-term mating and a focus on long-term gains (Brumbach et al., 2009). Early environments with high instances of adversity (e.g., abuse, neglect, and familial conflict) orient individuals more toward a fast life history strategy that favors immediate and short-term gains, including short-term mating (Brumbach et al., 2009). This may accelerate reproductive success by motivating individuals to have an earlier sexual debut, engage in higher amounts of casual sex, and thus a greater number of sexual partners (Ellis et al., 2003; Simpson et al., 2012).

Men tend to have fast life history strategies more often than women, but substantial variability exists among the sexes. Sexual minority women, particularly bisexuals, are exposed to more early adversity (Alvy et al., 2013; Austin et al., 2008; Hughes et al., 2014; Jun et al., 2010). These early adverse experiences may cause a subset of women to orient toward a faster life history strategy, leading to an early sexual debut, greater interest in casual sex, and more lifetime sexual partners (Goodenow et al., 2008; Tornello et al., 2014; Xu et al., 2010).

Although LHT originally made no predictions regarding same-sex behavior, Luoto et al. (2019) proposed that the behaviors of some nonheterosexual women arose from elevated androgen exposure, which in turn promotes fast life strategies. These authors argue that femme lesbian women are exposed to a small degree of prenatal androgenization and masculinization, whereas butch lesbian women have a proportionally more masculinization of the brain. Although they provide substantial support for their claims, this theory is not without critique. Most importantly, data indicate that bisexual women report more fast life history indicators than do lesbian women (see Diamond & Alley, 2019). LHT provides an excellent theoretical background for sexual behavior but needs further investigation to fully understand its applications to sexual minority men and women.

Concluding Comments

The existing literature highlights the tremendous variety in the sexual behaviors and mating strategies observable across individuals, genders, cultures,

populations, and ecologies. Research on human sexuality and mating has highlighted the importance of distinguishing between sex and gender, and within these categories distinguished between sexual identities, sexual preferences, and diverse sexual behaviors. Within behavioral repertoires, some people display exclusive and consistent sexualities and others have incidental experiences that vary throughout the life course, further highlighting these variations both within and between individuals. The current chapter reviews different ways to conceptualize sex, gender, and sexual orientation, and provides examples of same-sex sexual orientations and behaviors seen across cultures. We reflect on mating preferences of LGBTQ people when seeking partners/mates and examine these patterns from evolutionary perspectives that have been offered to explain same-sex sexual behavior from an adaptationist or by-product perspective. Overall, we advocate for the importance of considering environmental, social, ecological, and evolutionary factors that concomitantly impact sexual orientation and the mating strategies of people across diverse sexual and gender identities.

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PART III

Mate Competition

CHAPTER 13

Contest Competition for Mates and the Evolution of Human Males

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Abstract

Accumulating evidence suggests that the phenotypes of human males were shaped by contest competition, the mode of sexual selection in which mating opportunities are obtained by using force or threat of force to exclude same-sex competitors. Phylogenetic, paleontological, and archaeological data indicate a great antiquity for male–male violence in our lineage, and human males possess a constellation of traits that suggest specialization for contest competition. Relative to females, males exhibit greater stature, muscle mass, strength, speed, aerobic capacity, ability to dissipate exercise heat loads, craniofacial robusticity, pain tolerance, risk-taking, behavioral displays of physical prowess and acuity to the formidability of same-sex conspecifics, outgroup discrimination, and a propensity to participate in dyadic and coalitional violence. Parallel evidence suggests that some characteristics that distinguish hominins from the other great apes increase formidability in fights (e.g., handheld weapons, habitual bipedalism, and proportions of the hand and face) or function to increase perceptions of dominance (e.g., low vocal frequencies). Many of these traits are consistent with having been shaped by contest competition over mates: they develop or elaborate at sexual maturity and predict success in male contests, mating, and reproduction. Although alternative evolutionary explanations for some of these sexually dimorphic traits are possible, the most parsimonious explanation is that they have been preserved by selection because they aided in contest competition among males throughout human evolutionary history. The evolutionary roots of much of the aggression, intolerance, and violence that plagues modern societies may ultimately lie in the selection that shaped our mating

system.

Key Words: aggression, dominance, sexual selection, threats, violence, warfare

The ubiquity of human aggression

In the week leading up to December 25, 1914, British, French, Belgian, and German soldiers in several locations along the Western Front of World War I temporarily ceased hostilities to mingle, exchange gifts, and sing to each other. The "Christmas truce" is emblematic of the human capacity for collaboration and kindness, even in the midst of conflict, and it has inspired numerous works of art, including an Academy Award-nominated film (Carion, 2005) and a Pulitzer Prize-winning opera (Puts, 2011). Humans stand above all other primate species in their prosociality and cooperativeness (Gintis, 2000; Hawkes, 2014; Richerson & Boyd, 1998; Tomasello, 2020). Yet, we are also all too familiar with the extent of human violence within and among modern societies and in the historical record (Pinker, 2011). Analysis of the archeological record indicates that human violence predates state societies and the invention of agriculture (Beier et al., 2018; Keeley, 1996; Lahr et al., 2016; Melbye & Fairgrieve, 1994; Walker, 2001). In a review of the archeological evidence of interpersonal violence, Walker (2001) concludes that "as far as we know, there are no forms of social organization, modes of production, or environmental settings that remain free from interpersonal violence for long." Evidence of interpersonal violence is also strikingly apparent in some of the earliest fossils of our species (Fernández-Jalvo et al., 1999; White, 1986). If a propensity to sometimes resort to violence to resolve conflict is a fundamental component of the human behavioral repertoire, and we adopt the goal of reducing violence in the future, then it is incumbent upon scholars of human evolution to explore the evolutionary basis of violent behavior in our species.

Agonistic behavior has diverse functions across species (King, 1973), but some of the most intense and conspicuous aggression is a product of sexual selection (Andersson & Iwasa, 1996; Darwin, 1871). Sexual selection favors traits that increase *mating success*, a term that refers to the quantity of copulatory partners, as well as their quality—for example, their fertility, resource-provisioning potential, or heritable fitness—and copulatory frequency (Andersson, 1994; Anthes et al., 2017; Rosvall, 2011). Darwin (1859, 1871) recognized two distinct forms of sexual selection: *contests*, in which members of

one sex use force or the threat of force to exclude same-sex competitors from mating opportunities, and *mate choice*, which favors sexual ornaments and displays for attracting members of the opposite sex. Later scholars came to recognize additional forms, or "mechanisms," of sexual selection, including scrambles, endurance rivalry, sexual coercion, and sperm competition (Andersson, 1994; Andersson & Iwasa, 1996). Despite this recognition, the vast majority of research on human sexual selection into the first decade of the twenty-first century focused on mate choice, and indeed mate choice was viewed by some prominent researchers as the primary mechanism by which human males and females competed for mates over human evolution (Puts, 2010).

The emphasis on mate choice was based partly on the perception that ancestral humans chose mates relatively freely. Yet, this may frequently not have been the case, particularly for females. For example, more than two thirds of extant hunter–gatherer groups in a large sample had parentally arranged marriages (Apostolou, 2007), and although females may sometimes circumvent kin limitations on partner choice (e.g., via "mock bride theft"; Ayres, 1974), phylogenetic analyses suggest that family members influenced mating among the earliest members of our species (Walker et al., 2011). Moreover, constraints on female choice are imposed not only by kin but also by unrelated males via sexual coercion (Thompson & Alvarado, 2012; Wilson & Daly, 2009), and especially by males' exclusion of rivals by force or threat (e.g., Hill et al., 2013). Indeed, the weight of evidence suggests that many aspects of the human male phenotype are best explained by an evolutionary history of using aggression and threats of aggression against other males to obtain mates. Here, we discuss evidence for past sexual selection and its intensity among human males and evaluate evidence for the importance of contests, both dyadic and coalitional, in shaping male phenotypes. We focus on anatomical and behavioral phenotypes but consider some psychological traits, as well, and finish by considering alternative factors that may have contributed to human male phenotypes, including sexual division of labor, female mate choice, developmental linkage, and phylogenetic inertia.

Intensity of Sexual Selection in Human Males

The intensity of sexual selection is the degree to which reproductive success depends upon mating success and can be characterized by the slope of the linear regression of reproductive success on mating success (Arnold & Duvall, 1994). This slope is referred to as the *sexual selection gradient* or *Bateman gradient* (Andersson & Iwasa, 1996). Because larger variances facilitate stronger

statistical associations, the variances in reproductive success and mating success are referred to as the *opportunity for selection* and *opportunity for sexual selection*, respectively (Janicke et al., 2016). For a given sex, the opportunity for selection and the opportunity for sexual selection are quantified as the squares of the coefficients of variation in reproductive success and mating success, respectively (Arnold & Wade, 1984); they are dimensionless measures of variation in reproductive and mating success. Opportunity for selection, opportunity for sexual selection, and Bateman gradient are thus frequently used metrics of sexual selection (Janicke et al., 2016) (table 13.1).

Bateman Gradients and Variance in Reproductive and Mating Success

When Bateman gradients, opportunity for selection, and opportunity for sexual selection are estimated in modern human populations, they indicate substantial sexual selection that is stronger in males than in females (Borgerhoff Mulder, 2009; Borgerhoff Mulder & Ross, 2019; Courtiol et al., 2012; Janicke et al., 2016; Jokela et al., 2010; Moorad et al., 2011). Yet, studies investigating these metrics in humans are not without limitations. For example, paternity is assumed based on marriage rather than being genetically confirmed, and thus extramarital mating and reproduction cannot be detected. Mate quality is generally not assessed, with the exception of age-related variation in fertility (Borgerhoff Mulder & Ross, 2019). Mate quantity and copulatory success are also difficult to quantify in humans (Pérusse, 2010). Data on number of copulations and their timing during mates' ovulatory cycles are typically unavailable, and previous studies have instead used number of spouses, with one study accounting for the separate contributions of spouse number and years married (Borgerhoff Mulder & Ross, 2019).

Despite these limitations, data on Bateman gradients, opportunity for selection, and opportunity for sexual selection clearly point to substantial sexual selection operating on human males in modern and recent historical times across a variety of society types. Parsimony suggests a significant influence of sexual selection over human evolution as well. Nevertheless, given recent changes in the human social environment, patterns of subsistence, technology, and mobility, coupled with wide cross-cultural variability in these factors, it is unclear how representative any modern society is of the evolutionary conditions that shaped human genotypes and phenotypes. This caveat may apply equally to traditional societies (Foley, 1995). These societies experience conditions that are similar in many ways to those in which humans evolved (Foley, 1995) but may be more egalitarian due to the advantages of food sharing (Gurven, 2004; Hawkes et al.,

2014; Ringen et al., 2019) resulting from the disappearance of Pleistocene faunal abundance (Koch & Barnosky, 2006) and perhaps relegation to relatively unproductive land by colonial powers (but see Cunningham et al., 2019).

Table 13.1 Evidence of Past Sexual Selection in a Species

- Bateman gradient
- Opportunity for selection
- Opportunity for sexual selection
- Sex differences in
  - Reproductive variance
  - Parental investment
  - Potential reproductive rate
- Operational sex ratio
- Mating system
- Sexual dimorphism and other evidence of design for winning mates

It has also been proposed that males should have greater variance in reproductive success compared to females when sexual selection is more intense among males (Arnold, 1994; Bateman, 1948). In general, this pattern has been observed across a variety of human societies (Brown et al., 2009; Chagnon, 1979), although two caveats should be noted. First, the difference (or ratio) between male and female reproductive variances may be less relevant to understanding the strength of sexual selection in humans than it is in most other species. This is because there is evidence for relatively strong sexual selection acting on human females both currently (Borgerhoff Mulder & Ross, 2019; Courtiol et al., 2012) and in the evolutionary past (Campbell, 2013; Cashdan, 1996, 1998; Low, 1979; Low et al., 1987; Schmitt & Buss, 1996). Thus, the comparison of male-to-female variances may underestimate the intensity of sexual selection among human males relative to species in which female sexual selection is less intense. The second caveat, already noted above, is that modern patterns are unlikely to perfectly reflect those in the evolutionary past. For example, between-group coalitional competition among human males (see section "Coalitional Aggression") would have produced a source of variance in male reproductive success that may be present to a lesser extent in modern populations, and in any case would not be measured when variance is assessed within groups as has been done previously.

Nevertheless, if male reproductive variance exceeded that of females over human evolution, then genetic estimates of female effective population size should generally exceed those of male size. Several studies have argued that this is the case (Dupanloup et al., 2003; Hammer et al., 2008; Labuda et al., 2010), although the opposite pattern seems to characterize the expansion of modern

humans out of Africa (Keinan et al., 2009; Musharoff et al., 2019), and the expansion of Indo-Europeans from the Pontic Steppe into Europe (Goldberg et al., 2017a, 2017b). Karmin et al. (2015) argue that the ratio of male-to-female effective population size dipped in many parts of the world during the middle Holocene, during the spread of farming. They attribute this to a social change that allowed wealthy males to monopolize power and reproductive success.

Although these results seem to support the idea of more intense mating competition among males within populations, this interpretation assumes that the male and female ancestors of each population were part of a single population far back into the past. At least for Europe, this is not so. Most European mitochondria belong to haplogroups H or J, which arrived in Europe about seven thousand years ago as immigrants from Anatolia (Bollongino et al., 2013). By contrast, most European Y-chromosomes belong to haplogroups R1a and R1b, which arrived in Europe 4,500 years ago as immigrants from the Pontic Steppe (Haak et al., 2015). Consider the decrease in male effective population size that seems to have occurred seven thousand years ago (Karmin et al., 2015). At that time, most of the mitochondrial ancestors of modern Europeans did not live in the same population with the Y-chromosome ancestors. Consequently, the difference in male and female effective population sizes tells us little about social behavior within any single population.

Several of the studies discussed above do not rely on mitochondria and Y-chromosomes but instead compare autosomes to the X-chromosome. Nonetheless, the same issue arises. Autosomes are split evenly between male and female ancestries, but the split is uneven for X-chromosomes. Autosomes and X-chromosomes will therefore respond differently to the separation of male and female ancestors. Only in Europe is there clear evidence that male and female ancestries separate into different populations as we look backward into the past. Yet similar events may also have occurred elsewhere. There is growing evidence of population replacements far back into the past (Rogers et al., 2020). Models that interpret male and female ancestries in terms of social behavior within a single population should thus be interpreted with caution.

However, several replacement events exhibit a sex bias (Goldberg et al., 2017a, 2017b; Keinan et al., 2009; Musharoff et al., 2019), which is consistent with the view that males may get disproportionate access to reproductive females by invading and supplanting local males. In Y-chromosome data, variation between local groups is often large, and variation within them small, suggesting a tendency toward patrilocal residence and small male effective population size (Zerjal et al., 2002). In a few cases, these patterns are so pronounced that authors have attributed widespread Y-chromosome lineages to

particular historical figures. One such lineage in Central Asia has been attributed to Genghis Khan (Zerjal et al., 2003), one in China to the founder of the Qing dynasty (Xue et al., 2005), and one in Ireland to Niall of the Nine Hostages (Moore et al., 2006). Although these attributions are controversial (Wei et al., 2018), the pattern in Y-chromosome and mitochondrial DNA variation suggests that there has been great variation in male reproductive success for thousands of years, providing good evidence for a long-term difference in patterns of male and female reproduction.

Parental Investment, Reproductive Rates, and Operational Sex Ratio

Given the limitations of the data reviewed above, it is important to consider additional lines of evidence, as well (table 13.1). Notably, the anatomical, physiological, and life history features that characterize a species' reproduction influence the intensity of mating competition. Many sexually reproducing species exhibit an asymmetry in parental investment such that one sex, usually females, invests more in producing and caring for offspring (Trivers, 1972). This asymmetry is particularly pronounced in mammals in which initial stages of development occur within the female and, after birth, young are provisioned for an additional period through maternal lactation (Farmer, 2003). Although humans are unusual mammals in that males contribute to parental care, the disparity in female versus male investment remains dramatic; human development requires approximately nine months of gestation, followed by one to three years of lactation and extended maternal childrearing, while a contrastingly small parental effort is required for males to reproduce (Eibl-Eibesfeldt, 1989; Geary, 2000). As a result, human males have a higher potential reproductive rate (Clutton-Brock & Vincent, 1991), and in natural fertility populations, there are more males available to mate than there are females able to become pregnant (Trivers, 1972). Consequently, the operational sex ratio (OSR; the number of sexually active males per fecund female) is skewed in a way that may tend to place males in competition for the relatively few available females (Clutton-Brock & Vincent, 1991; Emlen & Oring, 1977).

When considering the human OSR, it may be important to distinguish the *physiological* OSR, which includes all individuals capable of reproducing, from the *behavioral* OSR, which includes only those within the typical age range of reproduction (Marlowe & Berbesque, 2012); the behavioral OSR may be more relevant to sexual selection (Kokko & Jennions, 2008; Kokko et al., 2012). Using mean forager values where possible and demographic data from Hadza foragers otherwise, Marlowe and Berbesque (2012) estimated the human

behavioral OSR to be 8.6 and the physiological OSR to be 11.7. Regardless of the measure used, the human OSR falls below orangutans (OSR = 55.0) and gorillas (OSR = 83.8), which display some of the most extreme sexual dimorphism among primates and above chimpanzees (OSR = 4.5), which also exhibit substantial dyadic and coalitional contest competition (Mitani et al., 1996; Wilson et al., 2014). The human OSR therefore suggests the opportunity for moderately strong sexual selection among males.

Group Structure and Mating System

The intensity of sexual selection is also influenced by the spatial distribution of males and females. If females are social or otherwise spatially clustered, then individual or small groups of males may be able to monopolize multiple females, resulting in a polygynous mating system and intense competition to be one of the few breeding males (Emlen & Oring, 1977). However, if female groups are large, then such monopolization is difficult, and multimale–multifemale groups tend to emerge. In such groups, male mating competition often involves dominance hierarchies in which dominant males obtain more mating opportunities, especially with estrous females. In primates, sexual dimorphisms in canine teeth and body size tend to be lower in multimale–multifemale species than in species with single-male polygyny (Clutton-Brock & Harvey, 1984), suggesting less intense contest competition.

Although humans everywhere form large multimale–multifemale groups, human mating structure is not typical of such primates. This may reflect males' inability to monopolize estrous females due to concealed ovulation (Gangestad & Thornhill, 2008; Marlowe & Berbesque, 2012; Puts et al., 2013), which may facilitate male investment in mates and offspring by increasing paternity certainty (Strassmann, 1981) and promote relatively stable mating relationships between individual males and one or more females embedded within the larger social group. As in hamadryas baboons (Schreier & Swedell, 2009), males' proprietariness over their mates helps maintain these mating relationships (Daly & Wilson, 1988), but the human institution of marriage may reduce within-group conflict by providing a conventional solution to within-group contest competition (Blurton Jones et al., 2000). The importance of male–male coalitions within groups (Wrangham, 2019b) and in between-group competition (Macfarlan et al., 2014; Van Vugt, 2011) may further mitigate within-group conflict because group cohesion and the well-being of fellow group members become important to individual fitness, and because smaller coalitions can safely punish or kill despots within larger groups (Wrangham, 2019b).

As the acquisition of female mates is a common objective in between-group aggression in traditional societies (Chagnon, 1988; Keeley, 1996; Walker & Bailey, 2013), this suggests that sexual selection operating on ancestral human males may have favored both traits that contributed to within-group competitive success and those that contributed to success in between-group competition or warfare. Thus, another implication of the dynamics of mating competition among human males is that mating and reproductive success, and hence the intensity of sexual selection, are more thoroughly measured across groups that compete rather than exclusively within groups (e.g., the replacement of European males by those from the Pontic Steppe, mentioned above).

Considering only within-group mating, the human mating system may be described as exhibiting low-to-moderate polygyny. Approximately 85 percent of described societies allow polygynous marriage (Murdock, 1967), and on average, 21 percent of married females are married polygynously across forager societies (Marlowe & Berbesque, 2012). In societies with exclusively monogamous marriage, males remarry (Buckle et al., 1996) and reproduce (Jokela et al., 2010) after divorce at higher rates than females (though see Borgerhoff Mulder, 2009), with reproductive variances comparable to those in societies with polygynous marriage (Brown et al., 2009). Consequently, mating systems tend toward effective polygyny, even in monogamous societies (e.g., Courtiol et al., 2012; Hill & Hurtado, 1996; Jokela et al., 2010).

Environmental Potential for Mate Monopolization

Across species, the intensity of male mating competition also depends on aspects of a species' habitat and environment (Andersson, 1994), including aspects that influence the defensibility of mates or critical resources for mating (Emlen, 2008). Such defensibility can be operationalized by the dimensionality of the mating environment (Puts, 2010). Males may more effectively monopolize females in environments that are one-dimensional (e.g., burrows) or two-dimensional (e.g., land or seafloor), as opposed to three-dimensional environments (e.g., air, open water, or trees) where the region that must be defended is larger. Terrestrial environments may thus favor more intense contest competition, as in terrestrially breeding seals (Stirling, 1975) and turtles (Berry & Shine, 1980) relative to aquatically breeding species. In chimpanzees and bonobos, which inhabit both arboreal and terrestrial environments, males engage in more violent fights on the ground (de Waal, 1986, 1989: Goodall, 1986; Kano 1992; Wrangham & Peterson, 1996) and flee into trees to avoid fighting (de Waal, 1989; Goodall, 1986; Kano 1992). Hominins began to adapt to an

increasingly two-dimensional environment with the emergence of habitual bipedalism at the latest by approximately 4 million years ago (MYA) in *Australopithecus anamensis* (Harcourt-Smith, 2007), and perhaps as early as 7 MYA in *Sahelanthropus tchadensis* (Brunet et al., 2002; Guy et al., 2022; but see Macchiarelli et al., 2020; Wolpoff et al., 2002), 6 MYA in *Orrorin tugenensis* (Pickford et al., 2002), or 5.8 MYA in *Ardipithecus ramidus* (Haile-Selassie, 2001; Haile-Selassie et al., 2004). This shift in the human paleoenvironment is likely to have shaped mating behavior; the new terrestrial environment may have enabled ancestral males to restrict sexual access to mates to a degree that was infeasible in their more arboreal ancestors.

Functional Design for Male Contests: Types of Evidence

The foregoing suggests substantial Bateman gradients for ancestral human males, but for sexual selection to shape phenotypes, mating must also be nonrandom such that phenotypes affect mating opportunities. That is, the *mating differential* (relationship between the trait and mating success) must be nonzero (fig. 13.1). Indeed, some of the strongest evidence of past sexual selection can be observed in the apparent design of phenotypes for success in competition for mates. In particular, human males show evidence of functional design for obtaining mates through contests. When evaluating phenotypic evidence, one can consider two related questions: First, does the trait show evidence of past sexual selection (table 13.2)? Second, does the trait show evidence of function in contest competition (table 13.3)?

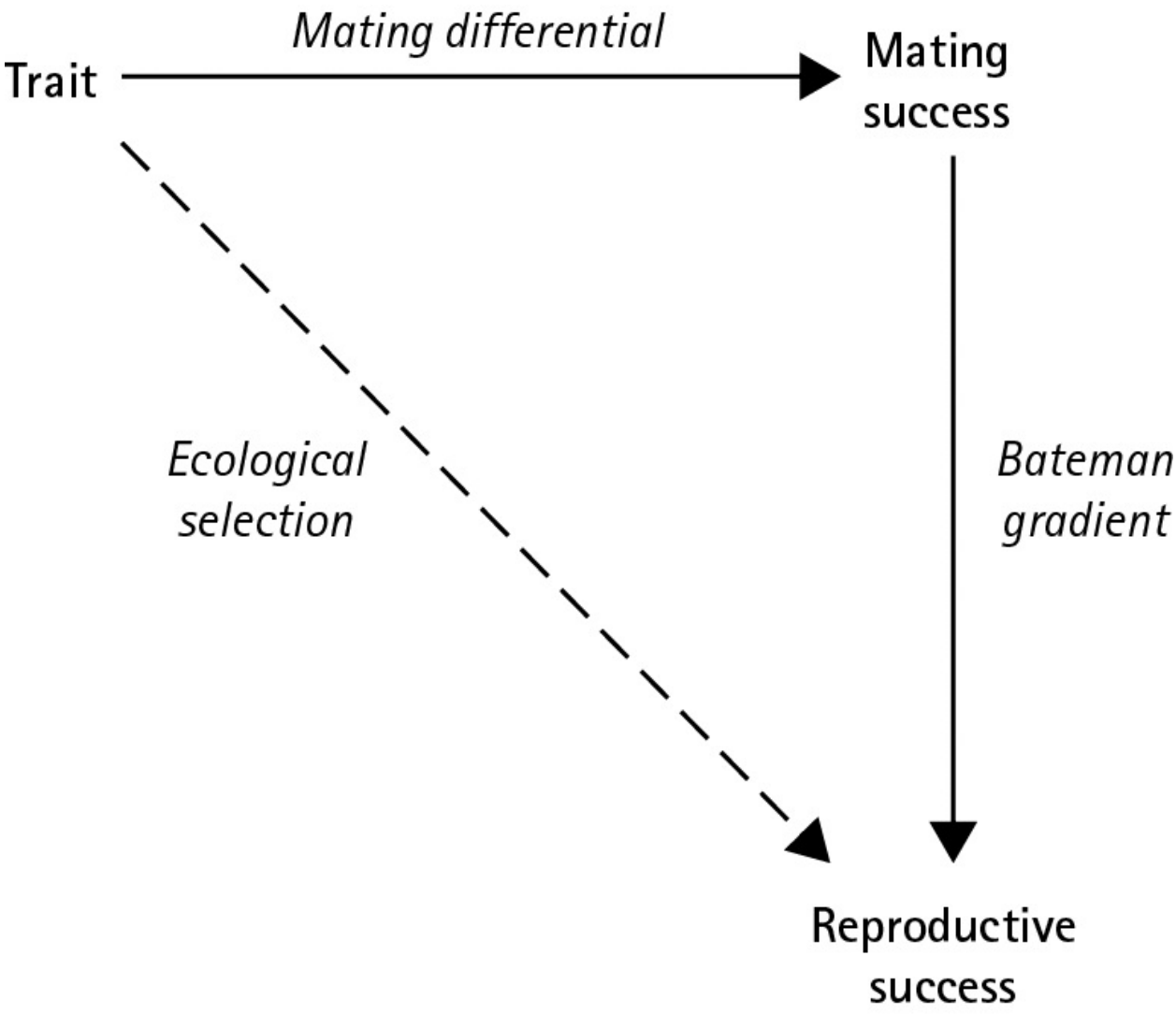

Figure 13.1 (after Hershaw & Jones, 2019). Sexual selection (solid lines) can be decomposed into the mating differential (relationship between trait and mating success) and the Bateman gradient (relationship between mating success and reproductive success). Ecological (non-sexual) selection on the trait is represented by the dashed line.

Evidence of Sexual Selection on a Trait

Table 13.2 Evidence of Past Sexual Selection on a Trait
1. Affects mating success 2. Affects success in one or more mechanisms of sexual selection 3. Sexually dimorphic 4. Develops or increases in expression at sexual maturity

Table 13.3 Traits Favored by Contest Competition
1. Propensity for physical aggression

2. Large body size
3. Strength
4. Anatomical weapons and armor
5. Behavioral displays of formidability
6. Anatomical threat displays

Several types of evidence suggest past sexual selection on a trait (table 13.2). First, if a trait currently influences mating success, then this suggests that it may have done so over its evolution. Second, if a trait affects success in one or more mechanisms of sexual selection (e.g., by attracting mates or winning fights with same-sex competitors), then this also suggests that the trait did so over its evolution. However, a crucial caveat is necessary regarding both of these types of evidence. If our species has a long and sustained history of sexual selection operating on males, then it follows that males should generally possess traits favored under sexual selection. This should have two consequences, both of which would attenuate current relationships between male phenotypes on the one hand and mating success and success under specific mechanisms of sexual selection on the other. The first is restricted phenotypic variance, which should decrease the precision of phenotypic characters in predicting relevant mating competition outcomes and reduce the effect sizes if variables are standardized. The second is that the strength with which present phenotypes can predict mating competition outcomes should be reduced not only because of phenotypic range restriction but also because of conditioning on past success: present phenotypes are disproportionately those that were successful in previous generations. For example, contest competition has presumably led to the evolution of enormous male elephant seals from an ancestral body size closer to that of females. Because all adult male elephant seals are now several times the size of females, there is almost certainly a weaker relationship between current male body size and mating outcomes than there would be if the full range of male sizes that existed over elephant seal evolution were represented in modern populations.

A third type of evidence of past sexual selection concerns sexual dimorphism. Because males and females tend to experience similar ecological conditions, if a trait exhibits a high degree of sexual dimorphism, then this suggests the influence of sexual selection (Andersson, 1994; Darwin, 1871; Lande, 1980). This is especially true if the trait exhibits evidence of design for winning mates in the sex in which it is more elaborate. Finally, sexually selected traits often develop or increase in their expression at sexual maturity when they can begin to compensate for their production and maintenance costs by aiding in competition for mates.

None of these lines of evidence is sufficient on its own. For example, if relevant aspects of the environment have changed, then a trait may currently influence mating success differently than it did ancestrally. In addition, different ecological selection pressures such as niche partitioning can produce sexual dimorphisms. Although this appears to be relatively rare (Andersson, 1994), it has been suggested that human sexual dimorphisms in body size and composition could be due in part to sexual division of labor (Kaplan et al., 2000). Sexual selection may also sometimes act similarly in the two sexes producing low sexual dimorphism (Hooper & Miller, 2008). However, in combination, these lines can provide strong evidence for past sexual selection.

Evidence of Functional Design for Contests

Traits shaped by contest competition will tend not only to show evidence of past sexual selection, including affecting success in contest competition specifically (table 13.2), but also to be one of several types of traits that aid in excluding same-sex competitors by force or threat across species (Andersson, 1994). These include behaviors such as same-sex aggression and threat displays and anatomical traits such as large body size and anatomical weapons (table 13.3).

Functional Design for Male Contests: The Evidence

Although there are numerous logical ways to present evidence for ancestral contest competition (fig. 13.2), we have chosen to organize taxonomically, beginning with traits shared by the broadest group under consideration, Hominidae (the great apes), and then interrogating progressively narrower taxonomic groups to bring the focus eventually onto our own species. This approach has the advantage of both providing perspective on similarities and differences with our closest living and extinct relatives and providing a sense of the relative recency or antiquity of relevant adaptations.

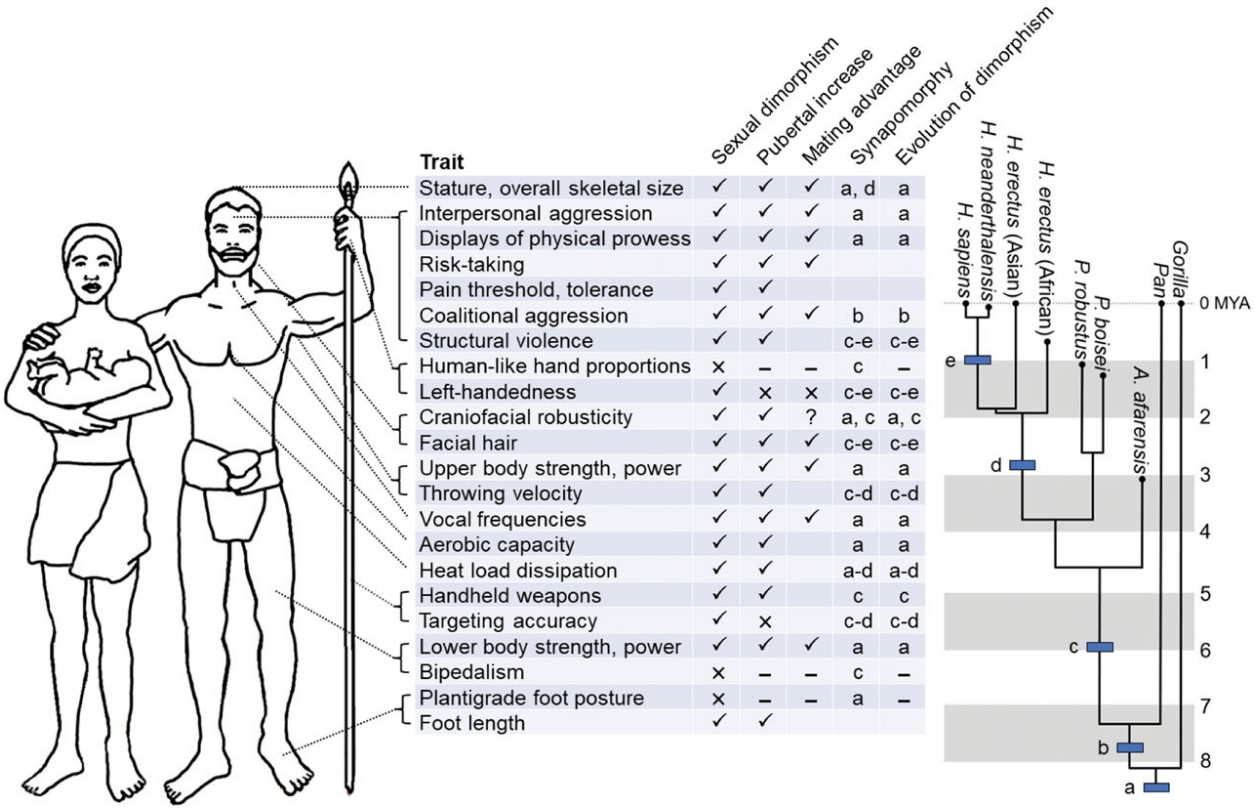

Figure 13.2 Human male traits for which there is evidence of function in contest competition. The table summarizes additional evidence (see text) of past sexual selection—whether the trait is sexually dimorphic, whether this dimorphism emerges or increases at sexual maturity, and whether individual differences in the trait currently predict variation in mating success in the expected direction—as well as an estimation of when the trait (synapomorphy) and trait sexual dimorphism evolved: in the common ancestor of a = Hominidae (great apes), b = Homininae (chimpanzees, bonobos, and all bipedal apes), c = Hominini (bipedal apes), d = *Homo*, e = *Homo sapiens* and *H. neanderthalensis*. Question mark (?) refers to mixed or partial evidence. Dash (–): not applicable. Blank cells indicate lack of evidence. Phylogeny modified from Parins-Fukuchi et al. (2019).

Hominid Characters That May Function in Contests

Humans are situated within the family Hominidae (great apes), which diverged from other apes (Hylobatidae) approximately 20.3 MYA (Perelman et al., 2011). In all living hominid species, males engage in intense contest competition and exhibit a suite of traits consistent with a history of male contests.

SKELETAL SIZE

Across most primate species, male contests favor large body size, producing sexual size dimorphism (Mitani et al., 1996). In all living hominids, males average larger postcranial skeletons than females, in terms of both overall length

and the lengths of individual elements (Gordon et al., 2008). The fragmentary fossil record indicates sexual size dimorphism dating back millions of years in bipedal apes, hominins (Plavcan, 2012), although levels of sexual dimorphism are debated. For example, in the best-represented fossil hominin, *Australopithecus afarensis*, which lived roughly three to four MYA, a level of sexual dimorphism commensurate with that of extant gorillas and orangutans has been inferred (Gordon et al., 2008; Lockwood et al., 1996; McHenry, 1991), although some have suggested more modest sexual dimorphism comparable to that of modern chimpanzees or humans (Reno & Lovejoy, 2015; Reno et al., 2010; Reno et al., 2003) (debate reviewed in Muller & Pilbeam, 2017). By the time of *Homo erectus*, whose existence covers most of the last two million years, sexual dimorphism had reached the approximate levels of modern *Homo sapiens* (Antón, 2003).

In modern humans, adult males are approximately 8 percent taller than adult females on average (Gray & Wolfe, 1980). This reflects both greater height growth velocity during the pubertal growth spurt and later pubertal onset in males, such that more growth occurs before epiphyseal fusion of the long bones and cessation of growth (Abbassi, 1998; Tanner & Whitehouse, 1976). Human sexual dimorphism in postcranial skeletal size exceeds that of chimpanzees, which have intense male dominance competition, but is substantially lower than that of gorillas and orangutans (Gordon et al., 2008), some of the most sexually dimorphic primates. Across twenty-eight human societies, higher societal levels of female status predicted decreased stature sexual dimorphism, perhaps due to stronger female choice against large, aggressive males (Gleeson & Kushnick, 2018) and/or weaker male intrasexual status competition in societies where females have more social power.

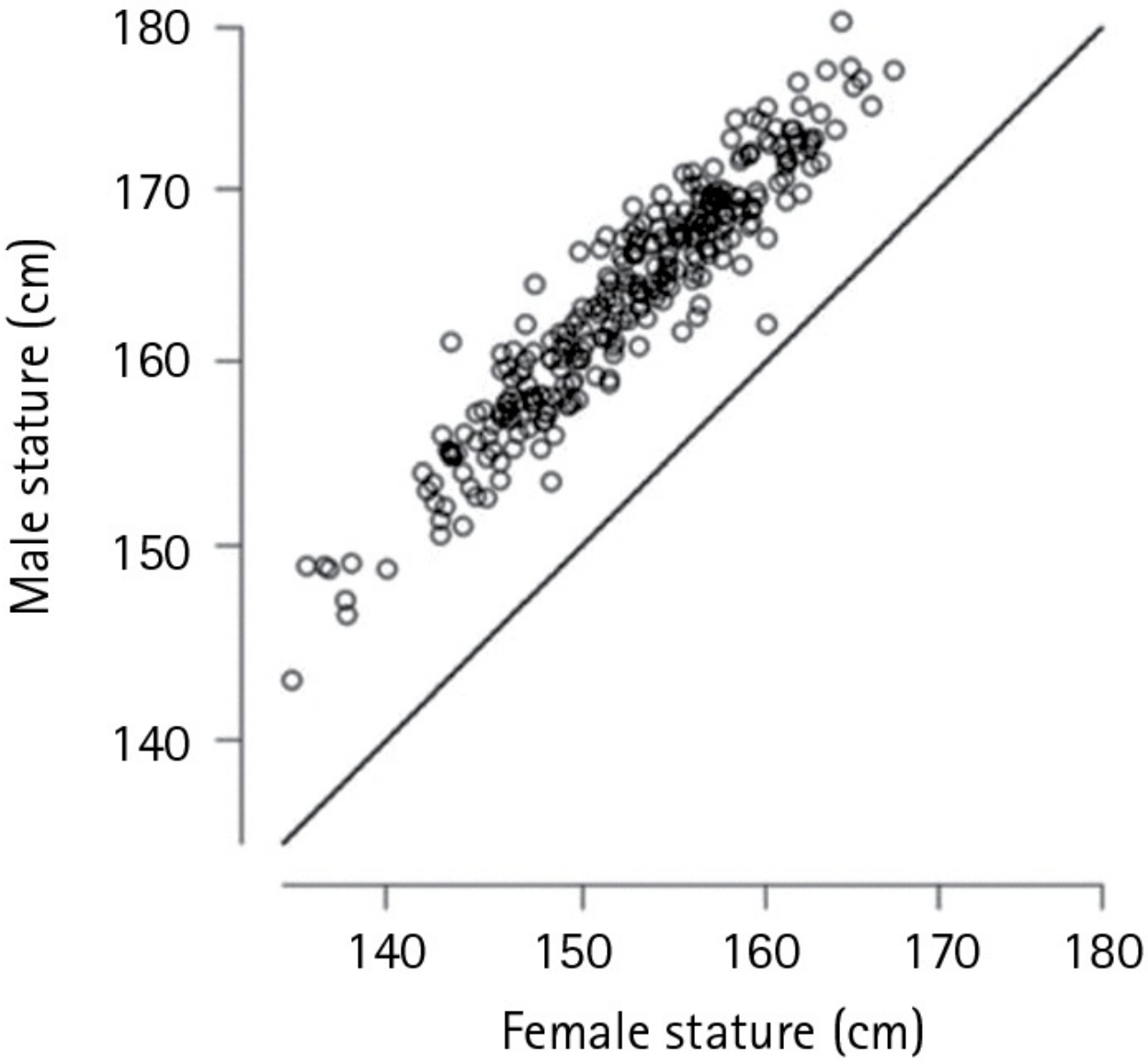

Figure 13.3 Sexual dimorphism in stature among human societies. Each dot shows the mean male and female statures of one human society. Sexual dimorphism is the vertical distance between each point and the solid 45-degree line. After Gray and Wolfe (1980) and Rogers and Mukherjee (1992).

In any case, variation across populations in stature dimorphism is surprisingly small, particularly given considerable variation in male and female averages (fig. 13.3). It is possible that the balance of natural and sexual selection favors a similar degree of dimorphism across populations. It is also possible that populations have diverged little in stature because sexual size dimorphism evolves slowly (Lande, 1980; Rhen, 2000). Most mutations that affect body size seem to affect the sexes similarly, and only a few contribute to sexual dimorphism (Rogers & Mukherjee, 1992). Consequently, there is more genetic

variance associated with mean body size than with the difference between male and female body sizes. Rogers and Mukherjee (1992) estimated that for three length variables (stature, span, and cubit), sexual dimorphism evolves nearly two orders of magnitude more slowly than does the mean of the two sexes. The slow rate at which sexual dimorphism evolves thus suggests the presence of strong and persistent differences in selection on male and female size over human evolutionary history.

MUSCLE MASS, STRENGTH, AND POWER

Males are also more massive and muscular than females in all living hominid species (Plavcan, 2012). A seemingly paradoxical characteristic of sexual size dimorphism in modern humans is that skeletal dimorphism is consistent with a primate species in which males have approximately 40–50 percent more body mass (Gordon et al., 2008), and yet overall mass is greater in males by only approximately 19 percent across forager societies (Marlowe & Berbesque, 2012) and 15 percent across a broader range of societies (Kyle et al., 2001; Lassek & Gaulin, 2009; Sherry & Marlowe, 2007; Wells, 2012; table 13.4). This comparatively minor sex difference in mass could suggest that male contest competition was weak over human evolution, and that humans are closer to monogamous species than to more polygynous ones in this regard (e.g., Fuentes, 2021; Schacht & Kramer, 2019). However, human females have uniquely large fat stores among primates (table 13.4; fig. 13.4a), and it is necessary to account for sex differences in body composition because divergent selection pressures operate on fat and muscle, and fat stores are unlikely to aid in fighting to the same degree as lean mass and muscle mass in particular (Lassek & Gaulin, 2009). Human males are approximately 33 percent larger than females in lean mass (table 13.4b), a difference that is more consonant with human skeletal dimorphism, and which exceeds those of monogamous nonhuman primates. Among the few nonhuman primates for which body composition data are available (fig. 13.4), human lean mass dimorphism is intermediate between species in which males maintain stable dominance hierarchies through agonistic encounters, such as chimpanzees and bonobos, and those with high-intensity intermale competition in which males are intolerant of other males, such as gorillas (Plavcan, 2004, 2012; Plavcan & van Schaik, 1992, 1997).

Human males additionally possess 61 percent more muscle mass overall and 75 percent more upper-body muscle mass than females (Abe et al., 2003; Lassek & Gaulin, 2009). As a result, among young adults, the average male has greater upper-body strength than 99.9 percent of females (Lassek & Gaulin, 2009). Sexual dimorphism in muscle strength and power appears to be particularly

pronounced in the muscles that contribute to striking. A study that compared male and female forward and rearward arm cranking power found pronounced male-biased sexual dimorphism in power of the muscles responsible for extending the arm forward (Morris et al., 2020). Male subjects exhibited 162 percent (3.5 standard deviations) more power in forward arm cranks versus 105 percent more power in rearward arm cranks (fig. 13.5). These results indicate higher sexual dimorphism in muscles associated with shoulder flexion and elbow extension power (i.e., those used in punching strikes).

Table 13.4 Total body mass, lean body mass, body fat percentage, and sexual dimorphism in primates.

Species	Study	Notes	Males				Females			
			Mass	Lean mass	Body fat %	N	Mass	Lean mass	Body fat %	N
Callithrix jacchus	Tardif et al., 2009	C, individually caged	0.386	0.274	9.7	32	0.412	0.283	13.2	32
Eulemur fulvus	Simmen et al., 2010		1.90	1.54	18.70	8	1.79	1.51	14.29	6
Gorilla	Zihlman & McFarland, 2000	C, FFM	191.9	147.7	23	2	99.5	82.4	24	2
Homo sapiens	Sherry & Marlowe, 2007	Tanzania, Hadza	53.20	47.56	10.60	238	46.30	37.50	19.00	23
	Kyle et al., 2001	Switzerland, White, FFM	74.00	59.42	19.70	2735	59.90	42.65	28.80	24
	Lassek & Gaulin, 2009	USA (approx. N), FFM	81.50	62.59	23.20	4461	68.50	45.28	33.90	50
	Wells, 2012	World (approx. N)	61.10	50.80	16.86	7975	53.50	38.70	27.66	63
		MEAN	69.17	55.69	19.10		59.91	41.74	29.97	
Lemur catta	Simmen et al., 2010	Some juveniles included	2.36	1.92	18.20	8	2.18	1.76	19.10	4
Macaca fascicularis	Pond & Mattacks, 1987	C	6.04	5.57	7.83	7	3.62	3.35	7.44	22
Macaca fuscata	Hamada et al., 2003	C, > 10y, median values			7					9
Macaca mulatta	Ramsey et al., 2000	C, individually caged	9.65	7.57	14.93	18	7.65	5.41	21.38	17
Macaca	Dittus &	Some	3.46	3.35	3.2	10	2.37	2.27	3.2	12

sinica	Gunathilake, 2015	juveniles included								
Pan paniscus	Zihlman & Bolter, 2015	C, trunk, limb fat only	42.68	42.67	0.00	7	34.28	33.08	3.48	6
Papio cynocephalus	Altmann et al., 1993	Fat % from 3 M, 13 F Mass from F ≥ 56mo	25.8	24.18	6.27	20	11.9	11.67	1.9	18

Note. Studies vary in methods of fat measurement, as well as whether lean mass or fat-free mass is estimated. Lean mass includes the small percentage of fat in bone marrow and internal organs known as "essential fat," whereas fat-free mass does not. One elderly, obese female gorilla was included in computing average female lean mass, but not mean female body mass or body fat percentage (see Zihlman & McFarland, 2000, for further description). Mass is reported in kg.

Key: C = captive, FFM = fat-free mass estimated instead of lean mass, mass dimorphism = male/female mass, lean mass dimorphism = male/female lean mass, body fat % dimorphism = female/male body fat %.

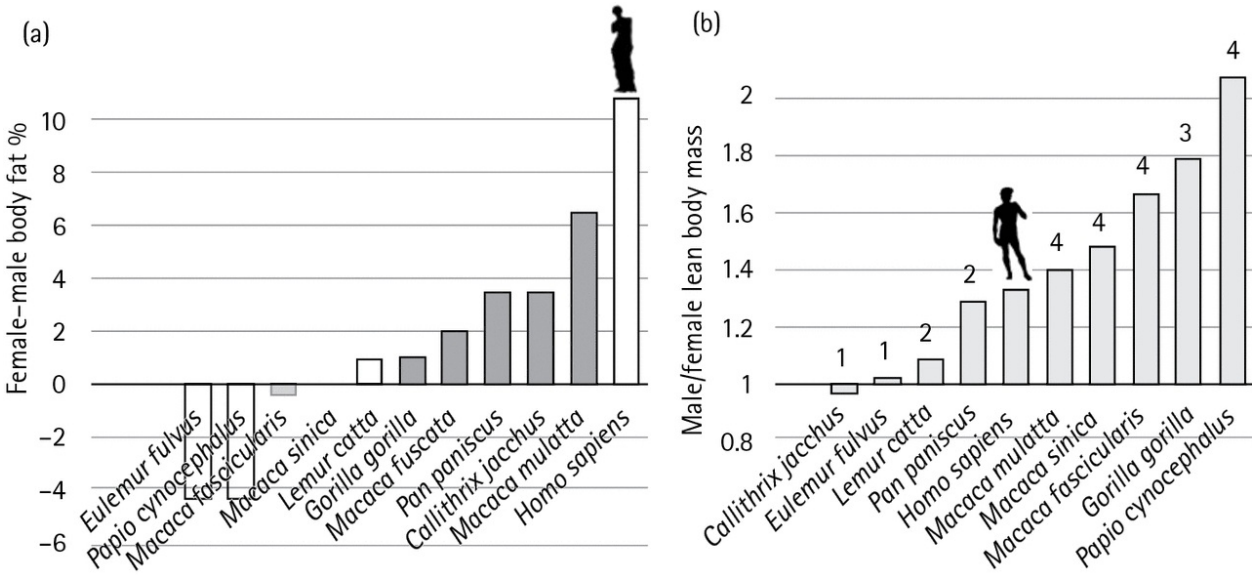

Figure 13.4a and b Sex differences in body fat percentage (a) and lean body mass (b) in primates. Females tend to store relatively more body fat than males in captive-living animals [shaded bars in (a)]. The human sex difference in body fat percentage exceeds that of other species for which data are available. Numbers above bars in (b) represent the level of male contest competition (1 = lowest, 4 = highest) using values from Plavcan and van Schaik (1992, 1997), or assigned according to their classification scheme (*E. fulvus* and *L. catta*). Humans are intermediate in lean mass sexual dimorphism among primates (b), a level of sexual dimorphism consistent with a species in which males maintain stable dominance hierarchies through agonistic encounters (level 2) or are intolerant of other males (level 3). See table 13.4 for sources.

In the lower limb, males possess 50 percent greater muscle mass (Abe et al., 2003), plus greater angles of muscle fiber insertion into the force-generating axis (Chow et al., 2000), permitting more packing of fibers and thus larger forces for the same muscle volume. These differences contribute to males having 65

percent greater lower-body strength (Lassek & Gaulin, 2009) and greater speed and acceleration: more than 45 percent higher vertical leap and more than 22 percent faster sprint times (Mayhew & Salm, 1990). The ability to apply forces to the ground can result in more powerful blows as well as aid in grappling (Carrier & Cunningham, 2017), and lower body strength and power have been associated with higher-level performance among male mixed-martial-artists (James et al., 2017).

SAME-SEX AGGRESSION

Males show high levels of intrasexual physical aggression in all living hominids (Muller & Wrangham, 2001). In humans, males are more physically aggressive than females across societies in both childhood and adulthood (Archer, 2004; Ellis et al., 2008). Male aggression peaks in young adulthood, which is consistent with the finding in many polygynous species that males delay the most high-risk confrontations until they are physically mature and prepared to enter the mating arena (Andersson, 1994; Archer, 2009; Geary, 2002). Across human societies, lethal violence among males is closely linked to mating competition, often being perpetrated when two males pursue the same female, or out of jealousy or suspicions of adultery (Chagnon, 1992; Daly & Wilson, 1988, 1990; Lee, 2012). Human males greatly outnumber females in both killing and being killed (Daly & Wilson, 1988), including both subsistence societies (Beckerman et al., 2009; Chagnon, 1988; Walker & Bailey, 2013) and industrialized nations (Daly & Wilson, 1990). Males account for an average of 95 percent of same-sex homicides with little variation across societies (Daly & Wilson, 1988), even as the number of homicides varies dramatically from one to another (Daly & Wilson, 1990). In several traditional South American societies, approximately one third of males die violently (Chagnon, 1988; Walker & Bailey, 2013). The cross-cultural universality of these sex differences and their similarity to the other great apes (Wrangham & Peterson, 1996; Wrangham et al., 2006), suggests that they characterized ancestral human groups as well.

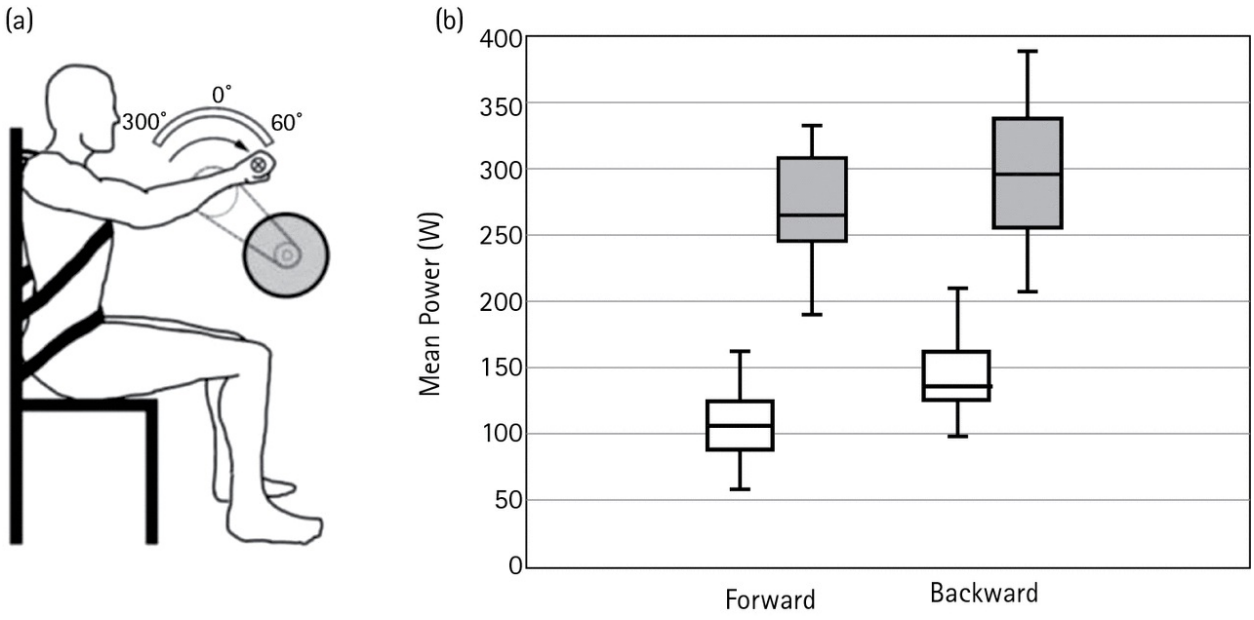

Figure 13.5 Male and female arm cranking power. (a) Illustration of testing apparatus. The arrow indicates the path of movement of the handgrip for a forward arm-cranking stroke. The gray shaded circle is the flywheel. Structural details have been omitted for clarity. (b) Box and whisker plots of subject data. Males (gray boxes, n = 20) had greater power than females (white boxes, n = 19) for both forward and backward cranking. Modified from Morris et al. (2020).

FOOT STRUCTURE

A final hominid trait that we mention now is the plantigrade foot structure that allows the heel to contact the ground during walking and standing and distinguishes the great apes from other primates (Gebo, 1992). It is likely that great ape feet are adapted for both arboreal vertical climbing and terrestrial quadrupedal locomotion (Holowka & Lieberman, 2018; Schmitt & Larson, 1995; Vereecke et al., 2003). Plantigrade posture increases locomotor economy in human walking but not running (Cunningham et al., 2010; Usherwood et al., 2012; Webber & Raichlen, 2016). Plantigrade foot posture may also improve performance when fighting with the forelimbs from a bipedal stance, a behavior shared by all hominid species (Carrier & Cunningham, 2017; Jablonski & Chaplin, 1993; Wrangham & Peterson, 1996). Applying forces to the ground with both the forefoot and heel greatly improves the capacity to exert torques on the ground, which has been demonstrated to increase striking and grappling forces and power in humans (Carrier & Cunningham, 2017). Selection for improved fighting performance may therefore also have been important in the evolution of plantigrade foot posture.

Hominine Characters That May Function in Contests

We now move down to the level of the subfamily Homininae, which includes chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), humans, and extinct bipedal human relatives, and which diverged from other hominids approximately 8.3 MYA (Perelman et al., 2011). Male hominines possess family-typical hominid traits associated with contest competition, including both absolutely and relatively large bodies, high muscle mass, and high levels of same-sex aggression. Sexual dimorphism in skeletal and body mass, as well as absolute mass, are lower in extant hominines than in gorillas and orangutans (Gordon et al., 2008; Plavcan, 2012).

COALITIONAL AGGRESSION

The hominine decrease in size and sexual size dimorphism may be attributable in part to multimale–multifemale social structures (Clutton-Brock & Harvey, 1984) but also to the presence of coalitional aggression (Wrangham et al., 2006). Benefits of coalitional success are shared among group members, whereas the costs of large body size are borne by the individual; hence, the marginal returns of producing and maintaining large, muscular bodies can be expected to diminish as success in group-level contests becomes more important to individual fitness. In both chimpanzees and humans, groups of males cooperate in the defense of females, as well as in attacking males from other groups. In chimpanzees, adult and adolescent females were the only individuals not observed to experience mortality as the result of intercommunity violence (Wrangham et al., 2006). Likewise, some archeological sites at which massacres occurred contain remains of many young adult males and few reproductive-age females, suggesting intermale violence and female abduction (Bentley et al., 2008; Willey, 1991).

There are notable differences in aggression between chimpanzees and humans, including protracted periods of nonviolence among rival human groups (Hames, 2019; Wrangham, 1999) and more frequent overt aggression but lower lethality in chimpanzees, such that chimpanzees and humans in subsistence societies exhibit similar levels of lethal aggression (Wrangham et al., 2006). Yet, both species share otherwise similar patterns of intergroup hostility and benefits from intergroup dominance (Wrangham & Glowacki, 2012). The archaeological record is also replete with evidence of violent and often lethal coalitional aggression among males (Andrushko et al., 2005; Keeley, 1996; Milner et al., 1991) stretching back beyond the advent of agriculture (Lahr et al., 2016). Aggression among allied groups of males, which presents early via boyhood competition (Geary et al., 2003), has likely long been a feature of human life (e.g., Bamforth, 1994; Frayer, 1997), and may also be a more primitive feature

of our hominine heritage (Brooks et al., 2021; Hames, 2019; Wilson & Glowacki, 2017).

Some scholars (e.g., Ferguson, 2013a, 2013b; Fuentes, 2021) dispute the antiquity and importance of coalitional aggression over human evolution, finding both a lack of evidence that coalitional aggression and contests in general were significant selection pressures on male phenotypes and a lack of material evidence for coalitional aggression itself. Ferguson (2013b) identifies four categories of material evidence for war: artistic representation of war, weapons, fortifications such as palisades, and skeletal evidence such as embedded projectiles. Such criteria mostly involve recent innovations and could provide evidence only for a somewhat narrow meaning of war. We have generally avoided the terms “war” and “warfare” when referring to coalitional aggression for this reason. It is unlikely that the attacks on other groups that occur in chimpanzees, or the dawn raids among the Yanomamö in which one or a few enemies are ambushed outside their village, would leave these forms of evidence. If male coalitional aggression was prevalent among our Pleistocene or earlier ancestors, it may nevertheless be difficult to detect in the fossil record.

Perhaps the strongest evidence that coalitional aggression is not a recent development is the apparent phenotypic design for contests detailed in this chapter, combined with the fact that coalitional aggression is observed in only two extant apes: humans and our closest living relatives. Nevertheless, intergroup competition may also have selected for a suite of psychological and behavioral traits that provide further evidence of its salience over human evolution. These include tendencies for males to contribute more to a group task when competing against other groups (Van Vugt et al., 2007), as well as tendencies observed in both humans and chimpanzees for males to classify others as ingroup versus outgroup, regard outgroup members as potential prey, attend to power asymmetries between ingroup and outgroup parties, attack outgroup parties ruthlessly when the perceived power asymmetry is large, and exhibit increased ingroup cohesion in the face of outgroup threats (Brooks et al., 2021; McDonald et al., 2012; Wrangham, 1999).

In humans, such tendencies relate to structural violence, a form of coalitional aggression in which political, economic, or cultural institutions and traditions enable and enforce inequalities among populations and/or groups (Galtung, 1969). The goal is suppression and/or exploitation of one group by another. Structural violence is facilitated by the human capacity for ingroup favoritism (ethnocentrism) and outgroup hostility (xenophobia). Although the extent to which individuals are ethnocentric and xenophobic in their views and actions is highly variable within and among populations, both phenomena appear to be

cultural universals or near-universals (Cashdan, 2001; Hammond & Axelrod, 2006). Given males' greater propensity to participate in coalitional fighting and their anatomical and physiological specialization for aggression, we can predict that relative to females, males will tend to be predisposed to xenophobia because these emotions and beliefs make it easier to marshal the fear and anger needed to attack other groups and be prepared to defend one's community from threats from other groups.

Some analyses of sex differences in ethnocentrism and xenophobia are consistent with these expectations. In a study of attitudes toward recent refugees, Australian males scored higher than females in level of prejudice toward refugees and perceived realistic threats to resources imposed by refugees (Schweitzer et al., 2005). Females also scored higher than males on positive attitudes toward refugees. A study of 3,704 White university students in the United States found that males scored higher than females on racist attitudes and were more supportive of policies that (1) reinforce racial inequality and (2) enforce racial segregation at the level of marriage and intimate relationships (Sidanius, 1993). A second study of university students found that relative to females, males were more (1) social dominance-oriented (degree of preference for inequality among social groups), (2) supportive of social and political ideologies that facilitate group-based hierarchy (e.g., racism), and (3) supportive of policies that have negative implications for intergroup relations (e.g., war, civil rights, and social programs) (Pratto et al., 1994). This study also found that social dominance-orientation was negatively correlated with empathy, tolerance, communality, and altruism. Thus, in addition to being more prone to use physical aggression to resolve conflict, human males also appear to be more emotionally and intellectually supportive of attitudes and policies that create and maintain discrimination and exploitation of outside groups.

LOW-FREQUENCY VOCALIZATIONS

Across species, male contests frequently involve displays and mutual assessment of formidability, often ending without a fight when one rival submits (Maynard Smith & Parker, 1976). Males of all hominid species exhibit behavioral displays that appear to function in deterring rivals (Muller & Wrangham, 2001). Males are expected to attend closely to the formidability and threat potential of same-sex competitors, defer to more formidable competitors, and use nonviolent means such as threats to obtain status and resources where possible (Richardson et al., 2021; Sell et al., 2009a; Sell et al., 2010; Watkins et al., 2010a; Watkins et al., 2010b; Wolff & Puts, 2010).

A trait that appears to function in threat displays across anthropoid primates is

low vocalization fundamental frequency (f_o), the rate of vocal fold vibration during phonation and the acoustic parameter closest to what we perceive as pitch. Phylogenetic reconstruction indicates that low male (relative to female) vocal f_o evolved in the common ancestor of catarrhine primates after their divergence from platyrrines (Puts et al., 2016) approximately 43.5 MYA (Perelman et al., 2011) and was subsequently elaborated or reduced depending on the intensity of male sexual selection, as indicated by mating system (Puts et al., 2016). Interestingly, chimpanzees and humans exhibited the greatest f_o sexual dimorphism of extant hominids—male-to-female ratios of 0.62 and 0.51 for chimpanzees and humans, respectively, versus ratios of 0.74 and 0.82 for gorillas and orangutans—though the highest levels of f_o sexual dimorphism among catarrhines were observed in *Cercopithecus* species, which exhibit single-male polygyny and territoriality (Puts et al., 2016).

In humans, correlational (Hodges-Simeon et al., 2010) and experimental (Feinberg et al., 2005; Puts et al., 2006; Puts et al., 2007; Rosenfield et al., 2020; Wolff & Puts, 2010) research show that lower f_o and formant frequencies (resonant frequencies of the vocal tract) increase perceptions of male formidability and dominance. As a result of elevated testosterone levels at puberty (Harries et al., 1997; Hollien et al., 1994), male vocal tracts and vocal folds grow 15 percent and 60 percent longer, respectively, than those of adult females (Fant, 1960; Titze, 2000), disproportionate to the 8 percent sex difference in stature (Gaulin & Boster, 1985; Gray & Wolfe, 1980). The larger vocal folds of adult males consequently vibrate at an f_o approximately half that of females during phonation. Similarly, males' larynges descend a full vertebra lower than females' at puberty (Fitch & Giedd, 1999), producing a longer vocal tract; lower, more closely spaced formant frequencies; and a deeper, richer-sounding timbre.

A widespread view is that low-frequency male vocalizations evolve in mammals to exaggerate the appearance of size (Charlton et al., 2007; Puts et al., 2016; Rendall et al., 2007). However, there is debate about whether such signaling in human males is partly honest (Aung & Puts, 2020; Aung et al., 2020; Puts et al., 2012a; Puts & Aung, 2019) or purely deceptive (Armstrong et al., 2019; Feinberg et al., 2018). Across ages and sexes, low f_o strongly indexes size, strength, and aggressive potential, given its association with male physical maturity (Aung & Puts, 2020). Within adult males, meta-analytic results indicate that low f_o modestly but significantly predicts greater height (Pisanski et al., 2014), testosterone levels (Aung & Puts, 2020; Schild et al., 2020), and upper-

body strength (Aung & Puts, 2020). Although f_o and formant frequencies did not predict fighting success in twenty-nine male mixed martial arts (MMA) fighters (Šebesta et al., 2019), a subsequent study analyzing 1,312 voice samples from 475 MMA fighters found that lower f_o and formant frequencies predicted higher factor scores related to fighting experience and body size in a multivariate regression model, explaining 3–8 percent of the variance (Aung et al., 2021).

The communication of formidability is likely to be multimodal and multicomponent, such that vocalization frequencies are but one set of many signals and cues utilized by competitors to assess formidability (Aung & Puts, 2020). Thus, the modest associations between f_o and measures of condition or formidability among adult males may be compatible with the modest associations between voice pitch and perceived formidability assessed in naturalistic contexts, such as by familiar peers (Hill et al., 2013) or from videos (Kordsmeyer et al., 2018).

Males have also been found to lower their f_o when speaking to a competitor if they perceive him to be less physically formidable and raise f_o if they perceive him to be more formidable (Leongómez et al., 2017; Puts et al., 2006). Lowering f_o may intimidate competitors but could also provoke dangerous retribution if dishonest. Lowering f_o evoked perceptions of aggressive intent (Zhang et al., 2020), and low-f_o male voices elicited aggressive cognitions and intent in males who perceived themselves to be more dominant and stronger (Zhang & Reid, 2017). Thus, some evidence indicates that both habitual f_o and f_o modulation honestly signal formidability and/or dominance. Regardless of their honesty, low vocal frequencies appear to function as threats to rivals in humans and other primates.

Hominini Characters That May Function in Contests

Hominini, the bipedal apes, are a tribe that includes humans and their extinct ancestors and relatives that diverged from chimpanzees approximately 6.6 MYA (Perelman et al., 2011). Because hominins have only one extant member, *Homo sapiens*, they are known only from this species and a scant fossil record.

BIPEDALISM AND UPRIGHT POSTURE

The defining anatomical character of Hominini is standing upright and walking and running on the hindlimbs. Many hypotheses have been proposed regarding the selective advantages of bipedal posture in early hominins: locomotor economy (Pontzer et al., 2009; Rodman & McHenry, 1980),

locomotor stamina and persistence hunting (Carrier et al., 1984), aquatic foraging/wading (Niemitz, 2010), thermoregulation in a hot environment (Wheeler, 1984), carrying (Iwamoto, 1985; Richmond et al., 2001), carrying infants (Etkin, 1954; Wall-Scheffler et al., 2007; Watson et al., 2008), reaching for food (Hunt, 1996), male provisioning of females (Lovejoy, 1981), arboreal foraging in the distal branches of trees (Thorpe et al., 2007), freeing of hands (Darwin, 1871), defense against predators (Kortlandt, 1963; Walter, 2004), throwing (Roach et al., 2013), and aggressive encounters (Carrier, 2004; Jablonski & Chaplin, 1993; Thorpe et al., 2002).

Regardless of which of these proposed selective advantages were most important in the evolution of habitual bipedalism in basal hominins, it is likely that the evolution of improved bipedal stability and agility increased the fighting formability of a lineage (i.e., basal Hominini) that was already committed to striking and grappling with the forelimbs (Carrier, 2011). Although bipedal locomotion is rare among mammals, many species, including nonhuman great apes (Thorpe et al., 2002), stand bipedally on their hindlimbs when they fight. Terrestrial vertebrates have evolved to work against gravity during locomotion which requires that the mobility and strength of limbs be oriented downward toward the substrate. Bipedal posture reorients the trunk from pronograde to orthograde, allowing quadrupeds to strike and manipulate an opponent with their forelimbs over the full locomotor range of motion; the range of motion that can presumably produce the most force and power. A study that used human subjects found that downward, lateral, and forward strikes from an upright bipedal posture were significantly more powerful than strikes from a simulated quadrupedal posture (Carrier, 2011). Importantly, subjects standing bipedally produced more than threefold more work in downward than upward directed strikes.

ADAPTATIONS OF THE HAND

The shape of the hand also distinguishes Hominini from the other apes. In comparison to those of the last common ancestor of chimpanzees and humans, the hands of hominins have shorter palms and fingers but longer thumbs (Almécija et al., 2015). Human-like manual proportions were present in basal hominins, the australopiths (Alba et al., 2003; Almecija et al., 2010; Kivell et al., 2011; Prang et al., 2021; Susman, 1994, 1998). Considerable evidence suggests that hominin hands are especially adapted to gripping tools such as clubs or hurled objects such as stones (Marzke, 1997; Marzke et al., 1992; Napier, 1962; Susman, 1998; Young, 2003, 2009), with later modifications at around 3.5 MYA in *Australopithecus* perhaps supporting the precision grips functioning in stone

tool manufacture (Prang et al., 2021). Another possible advantage of human hand proportions is that they allow the digits to be curled into a fist that provides protection to the delicate musculoskeletal elements of the hand when it is used as a club to strike during fighting (Morgan & Carrier, 2013). A study that used cadaver arms to measure in vitro strain in metacarpal bones during forward-punching and lateral-slapping strikes found that recorded strains were higher in strikes in which the hand was secured in unbuttressed and slapping postures than in the fully clenched fist posture typical of human punching (Horns et al., 2015). The evolutionary significance of the proportions of the hominin hand may be that these proportions improved grip strength and manual dexterity, at the same time enabling the hand to be used as a club during fighting. Functions in male contests may also help explain pronounced sexual dimorphisms in the human hand—for example, male metacarpals are longer and especially wider and stronger than female metacarpals (DeSilva et al., 2014; Lazenby, 2002), and size dimorphism has been documented in carpal dimensions (Kivell et al., 2013; Mastrangelo et al., 2011), although the biomechanical consequences of these sex differences are, to our knowledge, not understood.

CANINE REDUCTION, FISTS, AND HANDHELD WEAPONS

One of the most perplexing features of Hominini is that all hominins with the possible exception of *Ardipithecus ramidus* (White et al., 2009) appear to have exhibited substantial sexual size dimorphism suggestive of intense contest competition, and yet hominins possess reduced canine size and reduced canine size dimorphism. Contest competition often produces anatomical weapons, such as antlers, horns, and, in primates, large canine teeth. Yet, compared to other anthropoids, canine crown height is significantly reduced in great apes (Plavcan & van Schaik, 1997). Further reduction in canine size and a departure from the CP_3 honing complex characteristic of catarrhine primates is apparent in one of the earliest hominin candidates, *Sahelanthropus tchadensis* (Brunet et al., 2002), and this trend of canine size reduction extends through the Pliocene genera *Ardipithecus* (Suwa et al., 2009) and *Australopithecus* (White et al., 2000) to *Homo* after 2.5 MYA (Suwa et al., 2009). It is conspicuous that hominins lack the typical weaponry possessed by primates, including monogamous species such as gibbons, and yet they exhibit sexual body size dimorphism indicative of the type of intense male competition in which such weapons would be useful (Plavcan, 2012). Indeed, no living nonhuman primate exhibits this combination of large body size dimorphism with small canine size dimorphism (Plavcan, 2012).

The hypothesis that canine reduction in early hominins reflected a decrease in

male contest competition (Fuentes, 2021; Lovejoy, 2009) is challenged by the presence of significant male contests in all modern great apes, fossil evidence of substantial sexual size dimorphism in early hominins, and other evidence reviewed throughout this chapter. It has also been proposed that a shift in diet toward resources requiring stronger bite forces could have selected for decreased jaw gape and hence reduced canines (Hylander, 2013). Although this hypothesis remains plausible, the evidence for a general shift toward tougher foods in early hominins is mixed, as discussed in the next section.

Another hypothesis, compatible with a dietary one, is that canine weaponry was replaced by greater reliance on grappling and striking with the forelimbs from a bipedal stance (Carrier, 2011; Darwin, 1871). An increased importance of the forelimbs in fighting may help explain the reduction of canine size that began in Hominidae, and the evolution of hand proportions that allowed striking with fists (Carrier, 2011), and effective wielding of handheld weapons (Darwin, 1871; Marzke, 1997; Marzke et al., 1992; McHenry, 1991; Young, 2003, 2009) may explain the continuation of this trend throughout hominin evolution.

In addition to allowing a clenched fist, the adaptations of the hand that characterize the earliest hominins facilitate the transfer of energy from the forearm to a handheld object (Young, 2003, 2009), and the shift to habitual bipedalism and its associated orthograde posture not only frees the hands for tool use but also enhances the transfer of leg power into throws and strikes with handheld weapons (Young, 2003) and hence the injuriousness of physical blows (Carrier, 2011). If proto-hominin ancestors utilized handheld weapons, then these adaptations that increase the efficacy of handheld weapons would likely have diminished sexual selection pressures maintaining long canine teeth. Under weaker sexual selection, canines tend to reduce (Plavcan & van Schaik, 1997), probably in part because this allows a reduction in maximal jaw gape, which increases masticatory efficiency and bite force (Hylander, 2013).

Striking with handheld weapons or fists parsimoniously links multiple hominin features, including canine reduction, bipedalism, hand morphology, increased facial robusticity, facial dimorphism, and the retention of sexual size dimorphism (fig. 13.2). In an ape with considerable upper body strength and shoulder mobility, a clenched fist or a handheld rock, long bone, or heavy piece of wood could provide an effective weapon not only for males in competition for mates but also for both sexes in competition for resources with conspecifics, and handheld weapons could be utilized by both sexes against large carnivores at a carcass and in defense against predators.

A critical question concerns when hominins began to wield handheld weapons, and whether this coincides with canine reduction. Although the earliest

known weapons used by *Homo* are wooden throwing spears dated to 300,000 years ago (Schoch et al., 2015) and a possible wooden thrusting spear tip dated to 400,000 years ago (Allington-Jones, 2015), the emergence of manufactured stone tools by at least 3.4 MYA (Harmand et al., 2015; McPherron et al., 2010) suggests that handheld weapons were used much earlier. An ancestral hominin with male agonism and the capacity to shape stones into cutting implements would also likely utilize rocks, branches, and other materials in the environment as weapons. All extant great apes use tools (Panger et al., 2002; Rolian & Carvalho, 2017), and chimpanzees both make and use tools, including using branches in dominance displays (van Lawick-Goodall, 1968), throwing rocks (Goodall, 1964, 1986), and spearing small prey with sticks (Pruetz & Bertolani, 2007), implying that tool use characterized the last common ancestor of *Pan* and *Homo* (Prang et al., 2021) and suggesting that handheld weapons may have become a specialization of early hominins.

Across modern human societies, the manufacture, carrying, and use of weapons against same-sex rivals is common among males and rarer among females (Archer, 2004; Bègue et al., 2016; Dijkstra et al., 2012; Ellis et al., 2008; Murdock, 1965; Smith & Smith, 1995; Warner et al., 2005), a sex difference that may increase across puberty (Barnes & Latman, 2011). Due to the lethality of handheld weapons, modern human males are the most dangerous animals on the planet; even those living in traditional societies wield weapons capable of dispatching the largest carnivores (e.g., Hazzah et al., 2017) and largest land animals (Fa et al., 2016). The absence of large canines in early hominins should perhaps not be taken to imply a lack of weaponry.

CRANIOFACIAL ROBUSTICITY

For six decades, the distinctly robust faces of early hominins have been recognized as phylogenetically derived and argued to be functionally related to a diet that included hard, difficult-to-crush objects (Daegling & Grine, 1991; Jolly, 1970; Kay, 1985; Rak, 1983; Robinson, 1954; Strait et al., 2013; Teaford & Ungar, 2000) or abrasive foods such as grasses (Teaford & Ungar, 2000; Ungar et al., 2012). Although this hypothesis is appealing, biomechanical analyses of microwear patterns on postcanine teeth and carbon isotopes suggest that with the exception of *P. robustus*, australopiths did not consume significant amounts of hard objects (Grine & Daegling, 2017; Grine et al., 2012; Scott et al., 2005; Sponheimer et al., 2013; Ungar et al., 2012; Ungar & Sponheimer, 2011; Walker et al., 1981), and, with the exception of *P. boisei*, australopiths did not consume large volumes of tough foods such as leaves and grasses (Cerling et al., 2011; Sponheimer et al., 2013; van der Merwe et al., 2008). Underground storage

organs (USOs; roots, tubers, and bulbs) have been suggested as a possible early hominini food source that is mechanically tough, potentially requiring a relatively robust masticatory system (Dominy et al., 2008; Laden & Wrangham, 2005). However, if we assume that consumption of USOs involves intake of abrasive soil grit, then the relatively mild microwear patterns of analyzed australopith samples (possible exceptions being *A. africanus* and *P. robustus*) are largely inconsistent with significant consumption of USOs (Grine et al., 2012; Martínez et al., 2016). In addition, some of the most robust portions of the austalopith face (i.e., middle and posterior portions of the zygomatic arch, around the orbit, and the lingual and subcondylar regions of the mandible) tend to be overbuilt for the strains placed on the bone during mastication in primates (reviewed in Carrier & Morgan, 2015). A final caveat to the hard/tough diet hypothesis is the observation that robusticity of facial bones is the most sexually dimorphic aspect of the skull and one of the most dimorphic aspects of the skeleton as a whole in both australopiths and humans (Plavcan, 2002, 2003). Diet undoubtedly contributed to the facial structure of early hominins, but it is unclear which dietary sex differences could account for the markedly increased robusticity of male skulls.

Robust facial skeletons and dentition may also have provided protection against injury in male contests (Carrier & Morgan, 2015), with females exhibiting a correlated response to selection in males. When modern humans fight hand to hand, the face is usually the primary target (Brink et al., 1998; Le et al., 2001; Shepherd et al., 1990), and the bones that suffer the highest rates of fracture are the parts of the skull that exhibit the greatest increase in robusticity during the evolution of basal hominins (Carrier & Morgan, 2015). Many of the facial features that characterize early hominins may have evolved to protect the face from injury during fighting with fists (Carrier & Morgan, 2015) or handheld weapons. Specifically, the trend toward a more orthognathic face; the bunodont form and expansion of the postcanine teeth; increased robusticity of the orbit; increased robusticity of the masticatory system, including the mandibular corpus and condyle, zygoma, and anterior pillars of the maxilla; and enlarged jaw adductor musculature are traits that may represent protective buttressing of the face. If the protective buttressing hypothesis is correct, then the primary differences in the face of robust versus gracile australopiths may be more a function of differences in the intensity of contest competition than differences in diet, as is generally assumed.

Even though modern humans have less robust facial skeletons than earlier hominins, the more robust mandibles and brow ridges of human males compared to females may protect against catastrophic fractures of the face (Carrier &

Morgan, 2015; Puts, 2010), which is disproportionately targeted (Shepherd et al., 1988) and injured (Carrier & Morgan, 2015) in fights. Brink et al. (1998) examined 2,432 bodily injuries in 1,156 men and 325 women in Denmark for a one-year period in the mid-1990s, reporting 69 percent to have been craniofacial, with injuries in both sexes tending to be produced by blunt force at close range. Women also experience craniofacial trauma, often from male assaults (Novak & Hatch, 2009), but they generally do not experience commensurate levels of physical aggression (Campbell, 2013; Daly & Wilson, 1988) or cranial injuries and display less cranial robusticity (Carrier & Morgan, 2015; Shepherd et al., 1988). Similar sex differences in cranial trauma among Neanderthals and early Upper Paleolithic anatomically modern *Homo sapiens* suggest high levels of male violence targeting the skull in their common ancestor approximately 0.3 MYA (Beier et al., 2018).

SUITE OF *HOMININ SYNAPOMORPHIES* THAT ENHANCE FIGHTING PERFORMANCE

Some of the most diagnostic characters of hominins (bipedal posture, human-like hand proportions, and facial robusticity) improve performance in grappling and striking with the arms and perhaps especially with fists and handheld weapons. Plantigrade foot posture and disproportionate sexual dimorphism in upper body strength, both great ape characters, also improve grappling and striking performance in males. Nevertheless, each of these characters also enhances other functions: bipedalism aids in reaching for food, infant carrying, and throwing; bipedalism and human-like hand proportions facilitate general tool manufacture and use; some aspects of lower (but not upper) facial robusticity support forceful chewing; and plantigrade foot posture may reflect a compromise between vertical arboreal climbing and quadrupedal terrestriality, for example. Some of these traits, particularly those that are not sexually dimorphic (bipedalism, foot posture), certainly have served common functions in both sexes and may have been co-opted for fighting in males, or experienced additional selection for this function. Nevertheless, it warrants mention that the only proposed function that unites all of these synapomorphies is fighting performance.

Characters That May Function in Contests in Genus Homo

The genus *Homo* evolved by perhaps as early as 2.8 MYA (Villmoare et al., 2019), giving rise to several extinct species, including *Homo erectus*, which may actually represent several distinct species sharing a common ancestor with modern humans between 1.5 and 2 MYA (Parins-Fukuchi et al., 2019).

PROJECTILE WEAPONS

The use of projectile weapons such as hurled rocks and spears may have benefited from several derived anatomical features, including a fully lateral glenoid fossa, first appearing together in the ancestor of *Homo erectus* and *Homo sapiens* approximately two MYA (Roach et al., 2013). These features enable elastic energy storage and release at the shoulder, facilitating high-speed throwing. Selection for the use of projectile weapons may have contributed to both the male advantage in throwing velocity that is present in human infants and becomes very large in older children (1.5 standard deviations by age three, 3.5 standard deviations by age twelve; Thomas & French, 1985), even before large musculoskeletal sex differences develop at puberty (Young, 2009), and the 1.5 standard deviation male advantage in targeting precision, which appears to depend developmentally on early androgen exposure (Hines et al., 2003), is stable across puberty (Thomas & French, 1985) and remains after controlling for experience (Watson & Kimura, 1991).

LEFT-HANDEDNESS

Left-handedness is another "male" trait that appears to aid in contests. Although data on handedness in chimpanzees are equivocal (Corp & Byrne, 2004; Lonsdorf & Hopkins, 2005; Palmer, 2002), humans exhibit pronounced hand preferences, with males approximately 23 percent more often left-handed than females (Papadatou-Pastou et al., 2008), a difference established in early childhood (McManus et al., 1988). Handedness is heritable (Medland et al., 2009; Nurhayu et al., 2020), and left-handedness is associated with survival disadvantages (Coren & Halpern, 1991; Llaurens et al., 2009b), raising the question of why left-handedness persists at relatively high frequencies.

Raymond et al. (1996) proposed that left-handedness is maintained by frequency-dependent selection because the rarity of left-handedness gives left-handed males a fighting advantage. According to this hypothesis, right-handed males lack experience fighting rare left-handed males, whereas left-handed males gain abundant experience fighting right-handed males. Indeed, left-handed contestants are overrepresented and have a competitive advantage in interactive sports, particularly in hand-to-hand combat (boxing and mixed martial arts; Richardson & Gilman, 2019) and with handheld weapons (e.g., in the sport of fencing; Harris, 2010), but not in noninteractive sports, such as darts or bowling (Raymond et al., 1996). Homicide rates across eight small-scale societies strongly predicted higher frequencies of left-handedness, perhaps because the selective advantage of left-handedness increases with the importance of fighting ability to male fitness (Faurie & Raymond, 2005; but see Schaafsma et al., 2012,

for a society with high homicide but rare left-handedness).

FOOT LENGTH

Male foot length also exceeds that of females, both absolutely and relative to stature and body mass index (Domjanic et al., 2015; Fessler et al., 2005; Wunderlich & Cavanagh, 1999). The adult sex difference is attributable largely to the longer period of rapid foot growth in males prior to their later pubertal onset, when rapid foot growth ceases (Balzer et al., 2019; Busscher et al., 2011; Mitra et al., 2011). Foot length has been found to predict vertical jump displacement, a common measure of athletic potential, in males (Aiyegbusi et al., 2017; Davis et al., 2006; Fattahi et al., 2012) but not females (Davis et al., 2006), and it is also critical to the ability to apply torques to the ground, which are fundamental to the force and power of striking and grappling with the arms (Carrier & Cunningham, 2017).

PAIN THRESHOLDS AND TOLERANCE

Pain thresholds and tolerance may reflect adaptations that allow males to remain physically aggressive during contests. Physical pain signals actual or potential tissue damage and can motivate withdrawal from a damaging situation and protection of a damaged body part (Lynn, 1984). Organisms face trade-offs between remaining in a potentially fitness-enhancing situation but risking further damage and withdrawing, avoiding damage but missing an opportunity to increase fitness. The ratio of expected costs to benefits will vary between individuals and across contexts. Given stronger sexual selection among males compared to females, males are expected to engage in costlier, more injurious behaviors in contexts that can augment mating success, such as contests. Ancestral males who disengaged from or avoided contests may have escaped injury but obtained fewer mates. The experience of less pain from a given stimulus may also facilitate continued engagement in contests despite injury. If so, then males might exhibit less pain sensitivity and greater pain tolerance, perhaps especially during competition.

Indeed, relative to females, males can undergo more intense stimulation, such as physical pressure on the body for longer periods of time before experiencing pain, and can tolerate pain for longer (Fillingim et al., 2009; Riley et al., 1998; Schmitz et al., 2013). These sex differences are moderate to large (Fillingim et al., 2009; Riley et al., 1998; Schmitz et al., 2013) and emerge at puberty (Schmitz et al., 2013). Moreover, in one study, males experienced analgesia after competition against a same-sex competitors regardless of exercise, whereas females experienced analgesia only after exercise (Sternberg et al., 2001),

suggesting a function of high pain thresholds in male competition.

AEROBIC CAPACITY

Human males and females also differ in aerobic capacity, the ability of the pulmonary and cardiovascular systems to deliver oxygen to metabolically active tissues. The maximum rate of oxygen consumption is 25–30 percent higher in males than females in both high-performing endurance athletes (Billat et al., 2001; Davies & Thompson, 1979; Nevill et al., 2003) and army recruits (Knapik et al., 2001; Sharp et al., 2002). During puberty in males, aerobic capacity increases more than expected from body size alone, perhaps due to gains in fat-free mass and/or heart size (Janz & Mahoney, 1997; Williams & Armstrong, 1991). High aerobic capacity likely enhances performance in the male-dominated activity of persistence hunting (Bramble & Lieberman, 2004; Carrier et al., 1984; Liebenberg, 2006). Relative to females, Hadza forager males were found to walk greater daily distances at higher speeds and to expend more total energy and energy above that expended due to basal metabolism (Pontzer et al., 2015).

Aerobic capacity is also likely to be subject to strong selection in species in which males compete for access to females by fighting. Although the relationship between social dominance and aerobic capacity has not been studied in many species, a seminal study in red junglefowl (*Gallus gallus*), a species with intense male contest competition, found a twofold male-biased sexual dimorphism in the capacity to increase metabolism above resting levels and significantly higher values in this metric in dominant males (Hammond et al., 2000). A similar result has also been observed in tropical damselfish (Killen et al., 2014). In humans, aerobic capacity correlated strongly with competitive ranking in boxing (fig. 13.6) (Bruzas et al., 2014; Guidetti et al., 2002). Although studies of other combat sports (judo, karate, wrestling) have produced conflicting results, high aerobic capacity appears to be important to success in mixed martial arts competitors (James et al., 2016). Thus, greater aerobic capacity in human males may also reflect sexual selection acting on male fighting performance.

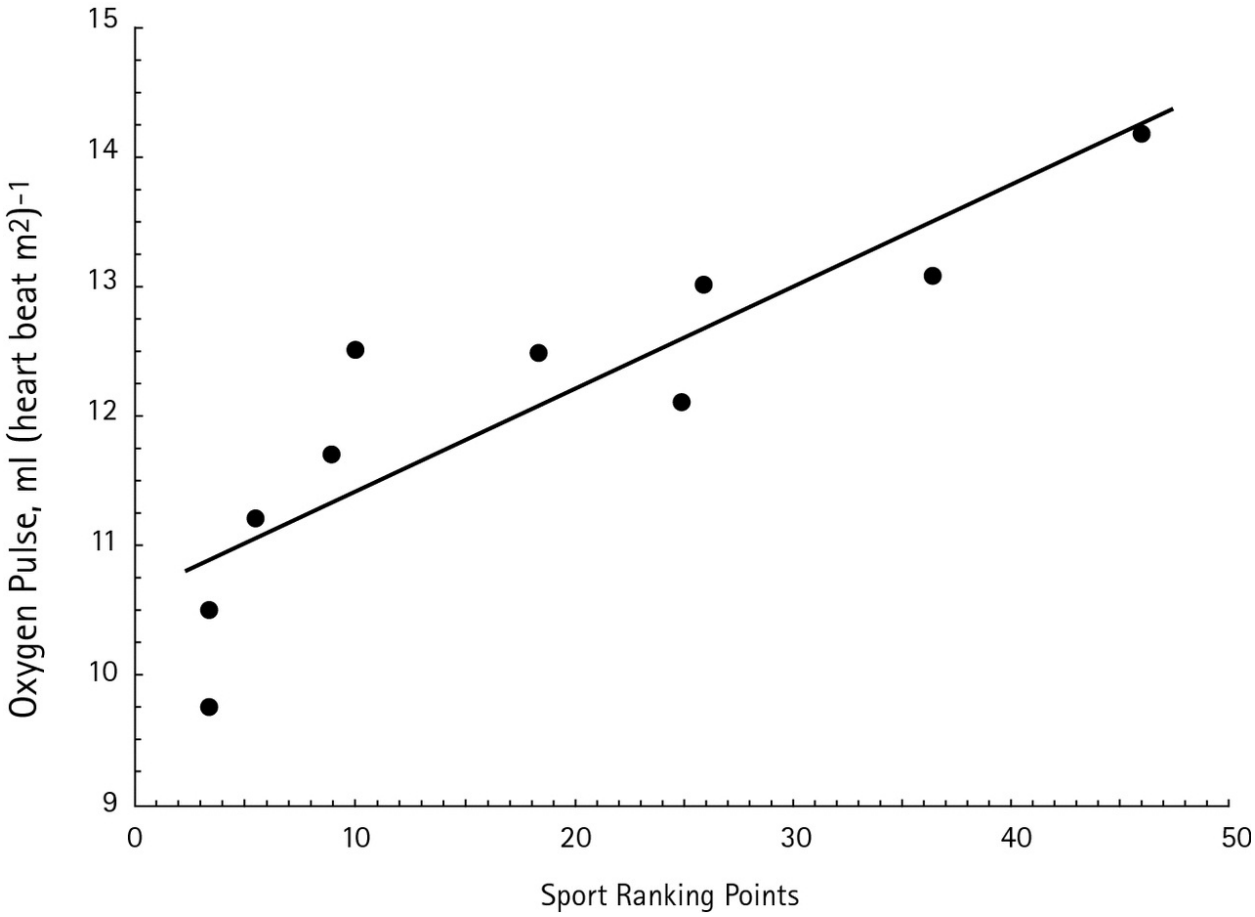

Figure 13.6 Correlation between boxers' maximal oxygen pulse and their sport mastery ranking points. Oxygen pulse is the ratio of oxygen consumption to heart rate and reflects the maximum aerobic capacity. Modified from Bruzas et al. (2014).

EVAPORATIVE COOLING

Consistent with the sex difference in aerobic capacity is a higher rate of thermoregulatory evaporative cooling in males. Among mammals the size of humans, the highest heat loads experienced by individuals are those produced not by hot environments but by vigorous exercise (Taylor, 1974). Although human females have more sweat glands per body surface area, the far larger sweat output of male glands results in a substantially higher maximum rate of evaporative heat loss in males (Gagnon & Kenny, 2012a, 2012b). Normalized to body mass, sweat production has been found to be 15 percent (Mehnert et al., 2002) to 45 percent (Hazelhurst & Claassen, 2006) greater in males than in females. Adjusted to surface-to-volume ratio, sweat production was shown to be 48 percent greater in males (Mehnert et al., 2002). Sweat production per body surface area and per gland, as well as sweat droplet size, increase at puberty in males (Falk, 1991; Falk et al., 1992; Meyer et al., 1992) but not females (Rees &

Shuster, 1981). Hairlessness and high rates of evaporative cooling are human characteristics that have been suggested to facilitate success in persistence hunting in the heat of the day; running prey animals with significantly lower heat dissipation capacity until they collapse from heat exhaustion (Carrier et al., 1984; Liebenberg, 2006, 2011). However, the higher heat dissipation capacity of males may also function to tolerate the high metabolic rates associated with physical combat.

DISPLAYS AND BADGES OF THREAT POTENTIAL

Human males utilize facial appearance (Carrier & Morgan, 2015; Sell et al., 2014; Sell et al., 2009a; Zilioli et al., 2015), muscularity (Durkee et al., 2018; Hill et al., 2013), and height (Stulp et al., 2015) to assess rivals' formidability, but some male characters, such as low vocal frequencies discussed above, appear to have been shaped by selection specifically to convey formidability.

Human males may display their formidability to rivals through risk-taking behavior and have been observed to increase the frequency of risk-taking when peers are present (Ginsburg & Miller, 1982; Morrongiello & Dawber, 2004), especially if those peers are male (Ermer et al., 2008). In a series of studies across two disparate societies, males who took more physical risks were perceived to be larger, stronger, and more violent (Fessler et al., 2014), suggesting that some risk-taking functions to intimidate competitors. Among the Meriam of Australia, the hunting of large sea turtles is physically demanding and potentially injurious, and may function to signal formidability to other males (Bliege Bird et al., 2001; Smith et al., 2003). Because turtle hunting is calorically inefficient, hunters give away the meat, and this altruism is not generally reciprocated, turtle hunting cannot be explained by optimal foraging or reciprocal altruism. Turtle hunters were respected by other males but not more attractive to females (Smith et al., 2003).

Males' greater average interest in playing and observing sports, both in the contemporary United States (Deaner et al., 2012) and across traditional societies (Deaner & Smith, 2013), may also reflect selection for displays of formidability—as well as for interest in competition and the predisposition to engage in activities that develop strength and skills useful in contests. Across fifty societies, males participated in 95 percent of all sports, females in only 20 percent, with males predominating especially in combat-related sports (Deaner & Smith, 2013). Among the Yanomamö horticulturists of Venezuela, contests often involve relatively less injurious modes of assessing formidability such as shouting matches, chest pounding duels, and side-slapping duels, and more rarely erupt into potentially fatal fights with clubs, axes, or machetes or shooting

with bows and arrows with lethal intent (Chagnon, 1988).

HAIR

Humans are among the most visually sexually dimorphic primates (Darwin, 1871; Dixson, Dixson, & Anderson, 2005), and some conspicuous male traits may function to increase the appearance of formidability. For example, beards and eyebrow hair are highly sexually differentiated (Darwin, 1871; Dixson et al., 2018), grow at puberty in males, and may project formidability by increasing the apparent size of the jaw and brow (Guthrie, 1970; Muscarella & Cunningham, 1996; Neave & Shields, 2008). Male faces with beards are generally rated as more dominant but not more attractive than the same faces clean-shaven (Dixson & Vasey, 2012; Gray et al., 2020; Muscarella & Cunningham, 1996; Neave & Shields, 2008), and beards have been found to facilitate recognition of facial displays of anger but not happiness (Craig et al., 2019). Across 154 primate species, such status "badges" were more likely to evolve in species with larger groups and multilevel social organization, perhaps because under these conditions, individual recognition is more limited, and social and physical conflict are more frequent (Grueter et al., 2015).

Facial hair may also play a role in protecting vulnerable regions of the facial skeleton from damaging strikes. One of the most commonly fractured facial bones in interpersonal violence, the mandible (Boström, 1997; Hojjat et al., 2016; Lee, 2009; Shepherd et al., 1990), is superficially covered by the beard. A recent study measured impact force and energy absorbed by sheep skin and fleece (used as a proxy for the skin and hair of human beards) and sheets of fiber epoxy composite (used as an analogue of facial bone) to test whether beards provide physical protection from blunt impact (Beseris et al., 2020). Total energy absorbed was 37 percent greater when the epoxy was covered with skin and fleece versus skin alone. As the authors of this study note, because sheep fleece is relatively dense, it is likely to be more protective against impact than are beards that are not both relatively thick and long. Additionally, it is possible that beards provide a protective advantage in reducing friction between the face and objects striking it from an oblique angle, which has not been tested.

Contests and Mating Success.

Human males thus possess a diverse suite of behavioral, anatomical, and physiological phenotypes that are consistent with an evolutionary history of contest competition. However, a necessary condition for design by sexual selection is that these phenotypes, and success in contests more broadly,

contributed to ancestral mating and reproductive success. Once again, it is informative to consider these relationships in modern populations with the caveats that modern conditions may differ in important ways from ancestral ones, and that a history of past selection for these phenotypes and restricted phenotypic variance should attenuate relationships with mating success in modern populations. We review associations with mating success with these caveats in mind.

Does Success in Contests Increase Mating Success?

As in chimpanzees (Manson & Wrangham, 1991; Mitani et al., 2010; Wilson et al., 2014; Wrangham, 1999), intergroup aggression in humans enables males to obtain territory and resources that may increase mating success (Bollig, 1990; Glowacki et al., 2017; Glowacki & Wrangham, 2015; Hames, 2019; Mathew & Boyd, 2014; Sellen & Hruschka, 2004). In other cases, the mating benefits of coalitional aggression are more direct. In particular, "wife raiding" appears to be a species-typical form of coalitional aggression, in which males forcibly procure female mates through "bride theft" (Ayres, 1974; Chagnon, 1988; Keeley, 1996; Peters, 1987; Sugiyama, 2014). Across ten traditional Amazonian societies, females were captured during 26 percent of raids occurring within a language family and 54 percent of raids occurring across language families (Walker & Bailey, 2013). Among the Waorani of Ecuador, males who went on more raids had fewer wives (Beckerman et al., 2009), though it is unclear whether raiding frequency decreased mating success or whether males with fewer wives were more motivated to raid as a means of obtaining wives. Subsequent research in this population found that participation in raids may afford opportunities for males and their offspring to marry the kin of males' raiding partners (Macfarlan et al., 2018).

Within groups, interpersonal physical aggression may help males obtain or defend mates directly, for example, by killing or injuring a competitor attempting to win the same mate (Lee, 2012; Marlowe, 2004), or attempting to steal one's mate (Chagnon, 1992; Lee, 2012). However, unlike chimpanzees (Wroblewski et al., 2009), savanna baboons (Alberts et al., 2006; Baniel et al., 2017), and most other primates living in multimale–multifemale groups, humans do not exhibit pronounced dominance hierarchies in which an alpha male achieves his position by physically defeating lower-ranking males individually. Human dominance relationships are more diffuse, and interpersonal physical violence among human males is approximately two orders of magnitude less frequent than in chimpanzees and bonobos (Wrangham, 2019a; Wrangham et al., 2006).

There is no consensus as to why humans evolved this difference with other anthropoid primates, but Wrangham (2018, 2019a, 2019b) suggests that it involved a reduction in reactive (or impulsive) aggression, as opposed to proactive (or premeditated) aggression. Wrangham further suggests that reduced reactive aggression may relate to several other changes that characterize the evolution of *Homo sapiens* approximately 300,000 years ago and that typify domesticated animals selected for docility. These include reduced body mass, shortening of the face and reduction in tooth size, reduced body size sexual dimorphism due to feminization of males, and reduced cranial capacity, collectively known as "domestication syndrome" (Leach, 2003). Wrangham (2019b) proposes that the evolution of linguistic abilities enabled males to cooperatively plan the execution of would-be despots, thereby reducing the advantage of dominance and leading to the social systems of modern human groups in which individual status is achieved largely via coalitional power (Gintis et al., 2015), or in which the majority prevents any individual from monopolizing resources (Boehm & Boehm, 2009). The evolution of concealed ovulation would also seemingly reduce the benefits of dominance and short-term mate monopolization in a primate living in multimale–multifemale groups (Marlowe & Berbesque, 2012).

Another key factor in these changes may have been the development of increasingly deadly weapons, including projectile weapons (Gintis et al., 2015), which likely favored a different set of behavioral adaptations, including arm speed (Roach et al., 2013; Walker, 2009) and targeting abilities (Hines et al., 2003), that weakened selection for overall strength (Walker, 2009), perhaps reducing sexual dimorphism in skeletal size and muscle mass. Several additional hypotheses identify factors, such as social selection for nonviolent mates or cooperative task partners, that may have contributed to the human domestication syndrome, each with advantages and disadvantages (Wrangham, 2019b). Although some of these hypotheses imply that contest competition has become less intense over the last 300,000 years of human evolution, it is also possible that intrasexual aggression merely became more strategic and coalitional and less focused on dominance hierarchies. Male deaths attributable to coalitional aggression are, if anything, higher among human foragers than among chimpanzees (Wrangham et al., 2006), and the evolution of putative threat displays, such as facial hair and deeper voices, and the development of deadlier weapons in *Homo sapiens* are also inconsistent with a major reduction in contest competition.

It is common in species with high potential lethality for males to evolve means of threat assessment and ritualized combat that avoid escalation to lethal

aggression (Eibl-Eibesfeldt, 1961). For example, male rattlesnakes engage in ritualized wrestling without biting (Eibl-Eibesfeldt, 1961). Likewise, mate acquisition and defense in human males may more frequently be accomplished indirectly through the threat of physical harm without resorting to costly violence. Play-fighting in juvenile males, physical fights without weapons, and sports (Deaner et al., 2012; Deaner & Smith, 2013) may represent forms of interpersonal physical aggression that serve these functions. Across societies, males who demonstrate physical formidability, strength, skill, bravery, and pain tolerance through ritualized activities from boxing and wrestling to Yanomamö chest-pounding duels (Chagnon, 1992) and land diving on Pentecost Island (Jolly, 1994) invariably win respect, admiration, and deference (Benenson & Abadzi, 2020). Such displays, as well as participation and success in coalitional aggression, all contribute to dominance (coerced social status; Henrich & Gil-White, 2001).

Dominance can aid in competition over contested resources, including mates and the resources useful in obtaining mates (West-Eberhard, 1983). In humans, the courtship attempts of dominant males may be less frequently challenged, and dominant males may interfere with the courtship attempts of other males with relative impunity (Hill et al., 2013; Mazur et al., 1994). Dominant males may also obtain resources useful in obtaining mates in a similar manner. Indeed, across several studies, physically formidable males, but not females, considered themselves entitled to better treatment (Sell et al., 2009b) and endorsed less egalitarian outcomes (Petersen & Laustsen, 2019). Dominance and fighting ability have been associated with increased male mating success in Western (Hill et al., 2013; Kordsmeyer et al., 2018; Wolff & Puts, 2010) and non-Western (Chagnon, 1988; Smith et al., 2003; von Rueden et al., 2011) samples. Success in competition with other males has also been shown to increase males' preferences for feminine female faces (Welling et al., 2013), suggesting that success in ancestral male–male competition may have increased access to desirable mates.

Success in contests also contributes to prestige (freely conferred deference; Henrich & Gil-White, 2001) because formidable males can make strong leaders and powerful allies and may also possess skills worthy of emulation (von Rueden et al., 2014). Experimental evidence suggests that social status is conferred upon formidable males in proportion to their being viewed as likely to generate benefits for the group via within-group enforcement and between-group representation (Durkee et al., 2020; Lukaszewski et al., 2016). Prestige may contribute to mating success in much the same way as dominance: prestigious males may, with relative impunity, court mates and acquire resources useful for

mate acquisition and interfere with the courtship and resource acquisition attempts of other males. Some evidence suggests that prestige obtained via formidability contributes to mating success. For example, in a small-scale Amerindian society, prestige was strongly correlated with dominance and predicted multiple measures of mating success, including earlier age at marriage, number of serial wives, number of extramarital affairs, in-pair fertility, and wife's attractiveness (von Rueden et al., 2011). Yanomamö males who killed an enemy in battle received an honorific title suggestive of high prestige and had more wives and offspring (Chagnon, 1988). In rural Senegal, males who participated in a traditional form of wrestling had more offspring and tended to have more wives, which Llauren et al. (2009a) attributed to elevated prestige. Across thirty-three nonindustrial societies, "social status," represented by variables related to both dominance and prestige, predicted reproductive success and mate quantity in both monogamous and polygynous societies, as well as mate quality in monogamous societies (Von Rueden & Jaeggi, 2016).

Finally, both dominance and prestige may contribute to attractiveness to potential mates or their family members involved in arranged marriages. Although dominant males may provide genetic benefits or protection to their mates, they also pose a risk of coercion and abuse (Borras-Guevara et al., 2017; Borras-Guevara et al., 2019; Li et al., 2014). Perhaps as a consequence, human females have been found to prefer prestige over dominance in a mate (Snyder et al., 2008).

Do Phenotypes That Function in Contests Increase Mating Success?

The evidence reviewed above indicates both that human males possess traits that function in contest competition and that success in contests elevates mating success. However, it is also relevant to evaluate mating differentials more directly: Do traits that function in male contests increase mating success? Evidence is generally supportive (fig. 13.2), with some exceptions (e.g., left-handedness; Faurie et al., 2006).

For example, a masculine, muscular body shape predicted greater numbers of sex partners (Frederick & Haselton, 2007; Hill et al., 2013; Lassek & Gaulin, 2009), particularly in short-term relationships (Rhodes et al., 2005), and earlier ages of sexual debut (Hughes & Gallup, 2003). Upper body size (Kordsmeyer et al., 2018) and strength (Gallup et al., 2007; Kordsmeyer et al., 2018) predicted mating success, and these associations were mediated by peer assessments of fighting ability from videos in German male university students (Kordsmeyer et al., 2018). Weight also predicted more sex partners among more than 31,000

primarily North American males (Frederick & Jenkins, 2015) and more wives and offspring among rural Gambian males (Sear, 2006b).

Taller males have reported more sex partners (Frederick & Jenkins, 2015; Mueller & Mazur, 2001) and marriages (Sear, 2006a). Relationships observed between male reproductive success and height are mixed (Mueller & Mazur, 2001; Pawlowski et al., 2000; Sear, 2006a) but appear curvilinear overall, with males of average or slightly above-average height leaving the most offspring (Sanjak et al., 2018; Stulp et al., 2012). This stabilizing selection may represent the opposing influences of sexual and ecological selection.

Mating success has also been associated with a variety of traits that influence perceptions of dominance. For example, displays of physical competitive ability such as sports performance (Faurie et al., 2004; Honekopp et al., 2007) and gang membership (Palmer & Tilley, 1995) have positively predicted mating success in Western samples, and physical risk-taking predicted mating success among the Meriam (Bliege Bird et al., 2001; Smith et al., 2003). A low vocal f_o has been associated with greater mating success in samples of American (Hill et al., 2013; Hodges-Simeon et al., 2011; Puts, 2005) and German (Kordsmeyer et al., 2018) university students, as well as with greater reproductive success in a sample of Tanzanian foragers (Apicella et al., 2007), but not in a sample of Namibian pastoralists (Atkinson et al., 2012). Among Bolivian forager-horticulturists, lower f_o predicted male reproductive success, and this was mediated by a component of mating success: wives' fertility rate (Rosenfield et al., 2020). Likewise, masculine facial appearance predicted mating success among Australian university students (Rhodes et al., 2005), and dominant facial appearance predicted mating success among German university students (Kordsmeyer et al., 2018) and eventual military rank and reproductive success among US military cadets (Muller & Mazur, 1997).

Alternatives to Male Contests

We have reviewed evidence that the phenotypes of human males were shaped by ancestral contest competition for mates. Human males exhibit each of the traits typical of species with male contests—size, strength, weapons, same-sex aggression, threat displays—as well as several others that appear to function in contests, such as pain tolerance. Many of these traits also show additional evidence of having been shaped by sexual selection insofar as they are sexually dimorphic and predict mating success, and many (e.g., deep voices, beards, and muscularity) also emerge at sexual maturity. Some exceptions are behaviors that

require years of practice to hone relevant skills: fighting, weapons use, behavioral displays of formidability, handedness, and coalition formation (e.g., Pellis & Pellis, 2007; Thomas & French, 1985)—all of which exhibit prepubertal sex differences, although the sexes may further diverge at puberty. However, many of these traits were likely influenced by other selective pressures or may have arisen as by-products of selection on developmentally correlated traits.

Sexual Division of Labor

Some human sexual dimorphisms may partly be products of a sexual division of labor that is ubiquitous across forager societies: Males spend more time hunting, especially larger game, and females spend more time gathering or hunting smaller game (Murdock, 1967). Such niche partitioning may have contributed to greater male size, strength, and weapons proficiency to the extent that these traits contributed to ancestral hunting success (Kaplan et al., 2000). However, this hypothesis leaves unexplained other male traits such as beards, deep voices, robust faces, and high levels of lethal same-sex aggression that are not easily understood as adaptations for hunting. The increased prevalence of left-handedness among human males is also more consistent with a role of ancestral fighting than with hunting; there is an overrepresentation of left-handed competitors in sports involving interactive contests, such as boxing and fencing, but not in targeting sports, such as darts and bowling, or in distance-throwing sports, such as javelin and shot put (Raymond et al., 1996). More importantly, male contests and sexual size dimorphism probably characterized the common ancestor of the great apes, and hence contest competition likely predates specialized hunting and the human sexual division of labor by several million years. It is therefore more plausible that the sexual division of labor is partly a consequence rather than the initial cause of these anatomical dimorphisms, although hunting likely imposed its own selection pressures.

Female Mate Choice

It is also probable that some aspects of the human male phenotype were strongly influenced by female mate choice. Because traits that evolve in contest competition are often costly to produce and maintain and are constantly tested by competitors, such traits may represent honest indicators of heritable fitness or the ability to provide direct benefits, and females may consequently evolve preferences for them (Berglund et al., 1996). Human males have been found to display athleticism and strength as tactics of mate attraction, verbally derogating rivals by impugning their strength and attempting to outshine them in sports or

other physical contests, especially when a potential mate is watching—tactics that are highly sexually differentiated (Buss, 1988; Buss & Dedden, 1990; Schmitt & Buss, 1996).

Masculine bodies, faces, and voices are sometimes (Frederick & Haselton, 2007; Gray & Frederick, 2012; Marcinkowska et al., 2019; Puts et al., 2012b; Sidari et al., 2020), but not always, (Scott et al., 2014; Shirazi et al., 2018) found to increase attractiveness to females. Nevertheless, the influence of these traits on ratings of dominance tends to be larger and more consistently positive than the effects on attractiveness (Frederick & Haselton, 2007; Hodges-Simeon et al., 2011; Puts et al., 2012b). For example, among Tsimané forager-horticulturists of Bolivia, lower male voice pitch increased perceptions of dominance to other males but decreased attractiveness to females (Rosenfield et al., 2020). Male facial masculinity is not universally preferred by females across human societies, whereas it more consistently conveys aggressiveness (Scott et al., 2014). Likewise, beards reliably increase perceptions of age, aggression, dominance, and social status across societies but generally decrease attractiveness to females (Dixson & Vasey, 2012; Gray et al., 2020; Muscarella & Cunningham, 1996; Neave & Shields, 2008). Across the suite of male secondary sexual characteristics, selection for success in contests may have been either attenuated or augmented by selection for attractiveness to females (Gleeson & Kushnick, 2018), but in general, these traits function more effectively in male contests than in mate attraction, and thus do not appear to have evolved primarily as sexual ornaments to attract mates. Furthermore, in samples spanning Western (Hill et al., 2013; Hodges-Simeon et al., 2011; Kordsmeyer et al., 2018; Mazur et al., 1994), traditional agricultural (Llaurens et al., 2009a), and preindustrial (Smith et al., 2003) societies, male mating success has been found to relate more strongly to social status (often indexed by wealth), dominance, and the traits that contribute to dominance than to attractiveness to females.

Development By-products

Another possibility is that some male traits represent developmental by-products of body size or gonadal hormones. Strength increases with body mass and height (Balogun et al., 1991), for example, although other male traits are not known to relate to body size (e.g., beards) or relate only weakly (e.g., voice pitch; Pisanski et al., 2014; and facial masculinity: Zaidi et al., 2019). However, even traits that correlate with size are far more sexually dimorphic than would be predicted from sex differences in size alone (Claes et al., 2012; Puts et al., 2012b; Zaidi et al., 2019).

Similarly, gonadal hormones such as testosterone and estradiol support the development of sexually dimorphic traits, so one may conjecture that these traits represent developmental side effects of gonadal hormones (e.g., Dunsworth, 2020). However, this confuses proximate and ultimate explanation, leaving unresolved the question of why humans have evolved to respond to testosterone by growing facial hair and longer vocal folds, or to estradiol by arresting long bone growth, for example (Font & Carazo, 2020; Galipaud & Kokko, 2020). Why instead do we not respond to testosterone by growing antlers, as in red deer (*Cervus elaphus*) (Suttie et al., 1995), or canines, as in many other primates (Van Wagenen & Hurme, 1950)? Why does testosterone not increase paternal investment, as in the California mouse (*Peromyscus californicus*) (Gleason & Marler, 2013), rather than having the opposite effect, as it does in many vertebrates, possibly including humans (Kuzawa et al., 2009; Puts et al., 2015)? Even closely related species can evolve markedly different responses to the same hormones. In general, sexually antagonistic selection pressures, such as sexual selection for male traits that would decrease fitness in females, produce intralocus sexual conflict (Bonduriansky & Chenoweth, 2009; Cox & Calsbeek, 2009). This conflict is resolved as selection favors sex-biased patterns of gene expression (Bonduriansky & Chenoweth, 2009), patterns that are orchestrated by gonadal hormones (e.g., Xu et al., 2012). An evolutionary history of male contests explains why, in humans, a particular constellation of sexually dimorphic traits may be developmentally linked to gonadal hormones and to each other.

Phylogenetic Inertia

It is also important to consider phylogenetic inertia—inheritance of our traits from ancestral species without necessarily experiencing selection for these traits in our own. Fossil and comparative evidence indicate that we inherited traits such as deeper male vocalizations, greater male size, individual and perhaps coalitional male–male aggression, and male facial robusticity from an ancient hominid ancestor, as discussed above. However, other traits such as beards and projectile weapons have evolved more recently, and although vocalization pitch was probably sexually dimorphic in our common ancestor with chimpanzees, sexual dimorphism has likely increased in our lineage (Puts et al., 2016). Even for traits such as greater male size and aggression that were likely sexually dimorphic in our common ancestor with chimpanzees, we would expect considerable reduction in modern humans if these traits were not functional over recent hominin evolution given their substantial costs. And yet, as discussed

above, men's physical aggression is equally if not more lethal than that of male chimpanzees (Wrangham et al., 2006), and we are more sexually dimorphic than chimpanzees in skeletal size and probably lean mass, as well.

Male contests parsimoniously explain human male phenotypes

It is fitting in a chapter commemorating Darwin's pioneering work on sexual selection to credit him for most of our central theses. Although many novel hypotheses and empirical studies have shaped our understanding of human sexual selection over the intervening years, we find support for Darwin's original inferences. In his own Victorian prose, "the greater size, strength, courage, pugnacity, and energy of man, in comparison with woman, were acquired during primeval times, and have subsequently been augmented, chiefly through the contests of rival males for the possession of the females" (Darwin, 1871, p. 605). Further, "as man gradually became erect, and continually used his hands and arms for fighting with sticks and stones, as well as for the other purposes of life … jaws, together with their muscles, would then have been reduced through disuse, as would the teeth" (p. 562).

A variety of human evidence, including sexual dimorphism in skeletal size and muscle mass, the OSR, and Bateman gradients in modern and recent historical populations, point to an ancestral selective regime characteristic of a primate with moderate to high levels of mating competition—substantially more intense than in pair-living species, perhaps also exceeding those of our closest living relatives, chimpanzees, but also below the levels of gorillas and orangutans. Likewise, hominin synapomorphies are consistent with a transition from using teeth to using fists and handheld weapons. It is easy to envision how, in the proto-hominin adaptive landscape, the evolution of hand proportions that allowed striking with fists and the innovation of handheld weapons would allow the male phenotype to shift from one local fitness maximum involving large canine teeth and biting to another involving reduced canines, adaptations of the hand, and bipedalism.

The development of handheld weapons represented a watershed moment. For the first time in primate evolution, individuals could aggress from a distance, keeping their most vulnerable body parts away from their enemies and reducing the advantage of anatomical weaponry. Very plausibly, this spurred a suite of other morphological and behavioral changes, perhaps including further reduction in canine size (Gintis et al., 2015), adaptations of the hand (Young, 2003), bipedal locomotion (Darwin, 1871), and increased locomotor economy (Carrier, 2004). Subsequent advancements in weapons design, coupled with adaptations

to improve throwing velocity and targeting accuracy perhaps by two MYA in *Homo erectus* would imbue male contests with increasing degrees of lethality. By the time of the evolution of our own species approximately 300,000 years ago, the aspirations of despots to monopolize conceptive matings may have been constrained by concealed ovulation, the threat of retaliation with deadly weapons, alliances between other males, and the importance of larger coalitions to the defense and acquisition of mates and resources. Hierarchical dominance relationships may have diminished, but contests continued to influence the mating success of human males, acting through coalitional aggression, interpersonal violence, and the threat of both—as well as the effects that formidability and success in contests had on prestige and mate attraction. Such selection pressures are evident in the constellation of adaptations that human males currently possess.

Alternative factors such as niche partitioning and female mate choice are also likely to have played important roles and are not mutually exclusive with contests. Aspects of the phenotype experience multiple selection pressures, as well as responding to selection on other traits to which they are developmentally linked. Yet again, most male secondary sex traits are best explained by contests, none is clearly better explained by other functions, and no alternative hypothesis accounts for the diversity of secondary sex traits in human males. Beyond the fact that contest competition is the most parsimonious explanation for these traits within humans, this hypothesis is also supported by analogy and homology, as many of these traits are used in contests in both distantly related species and in our closest living relatives.

Many researchers since Darwin have viewed a history of male contests as the likeliest explanation for the secondary sex characteristics of human males, and the supporting evidence has grown immensely since Darwin's time. There is more work to be done—for example, testing the relative importance of different mechanisms of sexual selection, as well as forms of ecological selection such as niche partitioning, in shaping male traits. Research identifying genes associated with the development of human sexual dimorphisms can also enable testing for signatures of recent selection (Arner et al., 2020). Nevertheless, humans appear to have experienced an evolutionary history of male–male violence, just as male sexual coercion of females appears to be part of our evolutionary legacy (Thompson & Alvarado, 2012). Humans have also evolved unprecedented cooperation, and human biparental care is exceptional among mammals. It can be tempting to focus on these more sanguine facts and ignore or deny the more repugnant ones, perhaps especially out of concern that doing otherwise might "justify cultural conceptions of masculinity, femininity, and rigid binaries of sex

and gender" (Dunsworth, 2020, p. 114).

It is important to emphasize that all traits have evolutionary histories, and that evolutionary explanations do not constitute moral justifications. But the oncologist presented with evidence of cancer does not render a diagnosis of remission merely because that is the desirable outcome. Likewise, we gain little by denying our evolutionary past. Understanding the evolution of human sex differences can lead to predictions about which traits will be developmentally linked, for example, suggesting shared underlying genetic and endocrine mechanisms, which has obvious relevance to disease phenotypes that differ by sex in prevalence or severity. Even more, we expect that acknowledging and understanding a legacy of male interpersonal and intergroup aggression can suggest developmental, sociocultural, contextual, and individual factors that may enable us to mitigate violent conflict and realize a more peaceful future.

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CHAPTER
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An Evolutionary Review of Female Intrasexual Competition

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Abstract

Research on female intrasexual competition has exploded over the last two decades. We provide an overview of the corpus of work, with the secondary aim of showing how this area conceptually grew over time. This chapter begins with historical perspectives of female intrasexual competition. We review how the field grew in response to scholars realizing the necessity of examining issues related to the promotion of female primates' individual fitness. Then, we describe women's aggression tactics and discuss how particularly indirect aggression is linked with women's competitive strategies, lowered physical confrontation, and a decreased potential for physical harm. We note that the topic of women's intrasexual competition has been overly dominated by mating-themed research, with far less attention toward ways that women compete in other domains that presumably heavily influence fitness. For example, only a few studies have examined competition among mothers, or on how mothers access limited resources for their children. Likewise, there has been little work on how women defend themselves against intrasexual aggression. We close with a discussion of future directions for research, with a focus on topics such as the importance of including non-WIERD samples in studying competition, competition among nonheterosexual women, the popularly discussed but highly academically neglected topic of "mommy judging," and competition among women who are postmenopausal.

Key Words: aggression, cooperation, fitness, mating, women

Setting the Stage: An Overview of Female Intrasexual Competition

> *What are little girls made of? Sugar and spice, and all that's nice;*
> *That's what little girls are made of.*
>
> *—nursery rhyme*

The British nursery rhyme clearly positions girls, and women, as kind-hearted, sweet, cooperative individuals who are nice. Although girls and women cooperate and behave with compassion and kindness, an evolutionary perspective leads to the conclusion that they are doing so because they are attempting to maximize their individual fitness.

Yet, simultaneously, popular culture routinely depicts girls and women as catty and competitive. Such works typically demonstrate the tactics that girls and women use to outcompete rivals for attention from prospective mates. Television shows such as *Riverdale*, *Gossip Girl*, and numerous "reality" shows such as *The Bachelor*, all emphasize women's mating competition as a core element of the storyline. Women are shown to spread rumors about, shun, and derogate rivals. All these behaviors are incongruent with the "sugar and spice" perspective.

The only way to rectify these opposing views of women is to recognize that women's behavior is functionally flexible; that is, women might be choosing the behavior with the greater net benefits on a context-by- context basis. The context may include many factors, such as broad cultural and social norms, but also situational features (e.g., the number of allies within close proximity, the quality of the current or potential mate, a woman's own status, her current fertility, whether the rivals are nearby, the level of threat rivals represent to her mating success).

Women, like all animals, are adaptation executors (Tooby & Cosmides, 1990); women's cognition and behavior have been shaped by recurrent challenges tributary to fitness, meaning that modern women might often behave in ways that may have historically maximized their survival and ability to have viable children who will themselves survive and bear children. Consequently, women must be viewed as active, capable strategists who seek to exploit opportunities and mitigate threats in their local environments. Although the earliest strictly evolutionary thinking may have assumed females were the relatively more "passive" sex, this view is not consistent among scholars taking an evolutionary approach to understanding human behavior (Buss & Duntley, 1999; but see, e.g., Tiger, 1977; for an historical overview, see Fisher et al., 2013). This tendency to examine women as such active agents has only become

increasingly apparent in evolutionary social science.

The Importance of Cooperation

We do not argue against the nursery rhyme's depiction of girls and women as "nice"; rather, we assert, first, that being and appearing nice can be an effective tactic for bolstering women's fitness outcomes (e.g., Garfield & Garfield, 2017; Hawley et al., 2008). Indeed, women do behave with kindness via, for example, sharing material goods, giving social or emotional support, and engaging in alloparenting. But, second, women are also, at times, not nice—that is, women are strategically noncooperative and competitive in ways that can also bolster their fitness outcomes. Flexibility is the cornerstone of survival and reproduction, and successful individuals must shift their strategies; they modify their involvement in cooperation or competition to ensure they have adequate resources and can rely on assistance from others. Like men, then, women must flexibly engage in cooperation and competition, but for women their flexibility is additionally affected by their roles as primary caretakers of offspring (Hrdy, 2009).

Women's high level of obligate parental investment means they must engage in intense cooperation, including with other women, because they greatly benefit from receiving assistance from alloparents and others who might help supply protection, information, or material resources. A child's father, though, is not necessarily the individual who provides the most childcare (see Sokol-Chang et al., 2017, for a review). A woman's male mate may be absent, noncommittal, unable to provide help, or become abusive, leading her to turn to other women for help (or to male kin and friends). For example, in foraging societies, childcare is typically provided by female relatives and close friends. Maternal grandmothers also cooperate by providing the primary provisioning that mothers and their children need (Hawkes et al., 1997). Among the Bwa Mawego of Dominica, older children, especially girls around the age of twelve, contribute to domestic labor at similar levels to adult women (Quinlan et al., 2003), freeing mothers to spend more time providing childcare. Likewise, for the Kikuyu of Kenya (Leiderman & Leiderman, 1974), child caretakers are usually females ages seven to twelve years and may be siblings, cousins, or neighbors. Hewlett (1991) documents that among many foraging societies, when an infant is held by someone other than the mother, that person is a close female relative or trusted female friend (see also Crittenden & Marlowe, 2008, for data on the Hazda). Indeed, even using a simple metric such as time holding an infant reveals a female bias, underscoring the notion that female allies are most often another

female's most probable alloparents.

Female friends can also cooperate with mothers. Barry and Paxson (1971), using a controlled sample of 186 societies, found that after mothers, the principle companions and caretakers of children were adult female relatives, then female children, then other females who are friends. Among the Ache, it is a mother's female friends and relatives who compensate for her decreased gathering time after she has given birth by either giving her food or providing childcare to enable her to gather food herself (Hill & Hurtado, 1996). Moreover, some views suggests that, due to relatively higher rates of female than male exogamy over our evolutionary history (Brown, 2014; Reynolds, 2021; but see Dyble et al., 2015), women would have been more likely than men to move into new groups of unrelated individuals, and thus would have needed to form friendships in lieu of having relatives (Lizarralde & Lizarralde, 1991). These new alliances may be built upon reciprocal altruism, with exchanges of material goods and assistance in the form of time and energy, all of which would improve the survival of both the mother and her child. Forming cooperative networks is indeed a critical component of women's evolutionary history.

Psychology has a long history of examining cooperation among women, but interestingly, an examination of fifty years of research on the topic suggests that there are minimal sex differences in overall amounts of cooperation (e.g., Balliet et al., 2011). Where such differences do appear, they are often in the opposite direction of the "sugar and spice" description; for example, men are comparatively more likely to band together in coalitional group warfare (Wrangham, 1999), have longer-lived friendships and be more likely to forgive friends' transgressions, and are generally comparatively more tolerant of genetically-unrelated same-sex others (Benenson, 2014). Thus, it is important to acknowledge that men, just like women, must be flexible in their strategies to cooperate or compete as needed. It is equally critical to recognize that, whereas the Western historical imagination and modern lay thinking might hold women and girls are "sugar and spice," this belief is not necessarily accurate. It fails to capture not only the lived experiences of many girls and women (Owens et al., 2000; Simmons, 2002; Valero, 1970). In fact, ask women and girls which people are most competitive *with them* today, and responses might imply women and girls are more competitive than men and boys. Further, the academic literature has long focused on men as being more competitive than women, but it has ignored that both sexes must be flexible in applying their cooperative or competitive strategies.

The Importance of Competition

Despite the benefits of cooperating, women must be able to engage in competition toward outcompeting rivals in contests for finite resources (e.g., mates, friends, tangible goods, resources for supporting children). Research on competition between women is not new. As we highlight in this chapter, the growing upswell of interest in women's competition is built upon evidence from a long history of examining female competition among nonhuman animals, and particularly nonhuman primates.

Competition between women for access to quality mates has been an area of considerable interest for the past two decades. For example, early work by Fisher (2004) revealed that during periods of high estrogen, women became harsher critics of other women's attractiveness as a form of intrasexual competition. Since then, the topic of women's mating competition has exploded and interest has spread to other areas, such as economics (via scarcity of women and competition for wealthy men; Ong et al., 2020), advertising (female models triggering aggression; Borau & Bonnefon, 2019), prenatal testosterone, and materialism (women with digit ratios indicating prenatal testosterone scored higher in believing material goods are a source of happiness when primed with competition; Nepomuceno et al., 2021), treatment toward refugees (fears over increased mate competition from novel rivals leads to hatred; Dancygier et al., 2019), or social inequality (women's limited access to resources increases time and attention to improving attractiveness; Blake & Brooks, 2019).

In this chapter, we primarily examine women's intrasexual competition for mates, and how it directly relates to fitness. We span a considerable range of topics, starting with an historical overview of the existing literature. We then discuss the current state of research, including competition that is not directly related to mating (but is nevertheless often tributary to fitness). One of our overarching goals is to create a foundation to present potential future directions for research. The last part of the chapter deals with specific suggestions for further work.

Historical Context

One of the pioneers in exploring female primate cognition and behavior, Sarah Hrdy (1999), detailed how competition between female primates, including women, is poorly studied, and yet they may be no less competitive than male primates. She reports that "no scientist has yet trained a systematic eye on women competing with one another in the spheres that really matter to them. The difficulty is not simply narrowness of vision and the mistaken assumption that female competition will take the same form as competition between males,

but also the subtlety of interaction between females" (p. 129; see also Burbank, 1987). From that time, researchers have made some significant strides in this area. For example, most evolutionary social scientists now take as given that female primates, including women, compete with one another, and that they do so via the full panoply of tactics—both cooperative and aggressive. This said, women seem to prefer to engage in more subtle, covert, and indirect tactics of aggression. Far from being merely a weaker version of male-male competition, such female intrasexual competition is highly effective. In this chapter, we briefly outline these strides and the current state-of-the-art on women's intrasexual competition.

We note that females of many species compete with each other to gain access to scarce resources that directly influence their survival and reproductive success. These resources include a wide array of limited items such as mates, habitats, status, and other resources necessary for reproduction (see Stockley & Campbell, 2013, for a review). Competition is usually highest among members of the same sex because they must most often benefit from and desire the same resources. Consequently, same-sex competition is a significant evolutionary pressure. Returning to Hrdy's sentiments—which have been echoed by other evolutionary social scientists in the intervening years (e.g., Benenson, 2014; Campbell, 2002; Fisher, 2017b; Hess & Hagen, 2006; Krems et al., 2015; Reynolds, 2021; Vaillancourt, 2013)—historically, research traditions have emphasized male–male competition, and particularly male–male mating competition. Only somewhat more recently has female–female competition research been systematically studied, again with early emphasis on mating competition (e.g., Liesen, 2013).

Why is much work on female intrasexual aggression relatively recent? First, we note that although evolutionary theory predicts female-female competition—and most obviously competition for desirable mates—historically, evolutionary meta-theories such as obligate parental investment (Trivers, 1972) have sometimes been popularly misunderstood as implying that women males compete for passively choosey females—a notion that evolutionary social scientists have not implied (e.g., Buss, 1985, 1987). Sex differences in human biology demand that women must substantially invest in their children, at least in terms of gestation and lactation. Men, however, are not faced with similarly high levels obligatory parental investment, meaning that women have a smaller reproductive potential, relative to men. Moreover, women's comparatively greater obligate investment—from gamete size through to lactation—further implies that males have potentially more to gain from competing for more numerous and novel female mates. Put somewhat differently, whereas there may

be similar net benefits of long-term romantic bonds for both sexes, on average, males seem to benefit more than females from short-term bonds (e.g., Buss & Schmitt, 1993), and might thus compete more frequently and ferociously for those mating opportunities.

A second reason for this focus on men's intrasexual competition is that the nature of men's and women's intrasexual competition is often different, such that men's modes of competition are typically more easily observable and overtly impactful (e.g., bruising and lethal), as compared to women's more difficult-to-detect modes of competition. Male primates (including men) generally compete in showy, observable ways (Benenson & Abdazi, 2020). Men have been repeatedly found to be more physically aggressive than women (e.g., Archer, 2004; Cashdan, 1998; Fry, 1998; Maccoby & Jacklin, 1974), although women also do compete physically (e.g., Campbell, 1992). For females, within-sex competition rarely involves escalating contests or combat using exaggerated secondary sexual characteristics, such as antlers (Clutton-Brock & Huchard, 2013). Thus, female aggression was less likely to be directly observed. Moreover, researchers had to develop alternatives procedures to capture women's aggression.

Yet from the beginning, evolutionary theory led to the prediction that female–female competition exists. The theory of sexual selection by Darwin (1871) comprises two parts: competition between members of the same sex for access to mates and intersexual selection, which is the process whereby individuals with a given trait are preferred by the opposite sex as mating partners. There has been ongoing debate about the mechanisms and consequences of sexual selection as displayed in female versus male animals, and whether sexual selection acts on females in the same manner (see Hare & Simmons, 2019). However, for our purposes, evidence does indicate that women are competing not for access to just for *any* mates but for access to *desirable* mates (see Fisher, 2013) who confer evolutionary advantages to potential offspring. Due to one sex having systemic preferences for potential mates possessing specific traits that advertise genetic quality or parenting ability, for example, these preferred features become prevalent within the population due to their being favored over time during mate selection. Further, they become dimensions over which to compete for access to mates, given that they are sought by the opposite sex. Evolutionary-minded research on within-sex competition has extensively relied on this model, consequently leading to considerable interest on all aspects of mating behavior. However, these findings reveal an early expectation that both men and women should be predicted to compete intrasexually, at least for access to desirable mates.

Indeed, substantial evidence reveals that women do compete for mates (see Vaillancourt, 2013). Most work in this vein begins from the premises that (1) men, as compared to males of most other species, provide significant levels of paternal care for children (Clutton-Brock, 1991), although care substantially varies among men; and (2) access to such care may be key for females' reproductive fitness. The result is that men who are good providers, and who display traits associated with provisioning such as generosity, commitment, and loyalty, are a scarce commodity for which women compete (e.g., Buss, 1989; Vaillancourt, 2013). Women are especially likely to compete for access to such desirable mates when there are high levels of maternal investment, when paternal investment is beneficial, and where there are large aggregates of individuals living together and competing for nearby resources (Apicella & Dreber, 2015). This situation is intensified by humans living in social groups composed of other women with their children, such that there is competition for limited resources that impinge on one's survival and that of their children.

The literature on female competition nevertheless retains a serious limitation. Specifically, the narrowness of this predominant focus on women's *mating* competition has often been at the exclusion of other important facets of human behavior that impact on women's reproductive success, such as parenting, sustaining high-quality affiliation partners, and defending themselves against same-sex aggression. For example, little research exists on how mothers compete for resources that directly affect their children's survival—and their own (but see Benoit & Fisher, 2019; Fisher & Moule, 2013; Linney et al., 2017). This gap is important because evolution rests on individuals' promoting their own fitness, and by necessity must include behaviors outside mating, such as self-survival (e.g., acquiring sufficient nutrition and avoiding dangers), biased investment in offspring (e.g., investing more in one child than other), or trade-offs between current and future offspring (e.g., deciding to commit infanticide to have possible increased reproductive success later). Likewise, whereas evidence suggests that sustaining close friendships can benefit female fitness (Rucas, 2017; Silk et al., 2003) and qualitative work reports the ferocity of girls' and women's competition for same-sex friends (e.g., Owens et al., 2000; Simmons, 2002), little work has explored if—and how—girls and women compete for friends (but see, e.g., Krems et al., 2021, 2022a; Vaillancourt & Krems, 2018). To illustrate these points, we know a good deal about the gossip women might deploy when competing with same-sex rivals for male mates (e.g., about beauty and sexual fidelity), but researchers have not identified friendship qualities potentially most valuable among women (but see, e.g., Williams et al., 2022), and whether denigrating these features might successfully help women compete

to attract and retain desirable female friends.

More recently, researchers have begun to work from the premise that, regardless of the contested resource, female–female competition takes distinct *forms* from those employed in male–male competition. Some such work asks, given the different forms of aggression females employ, how might female prospective victims defend themselves against these unique challenges posed by same-sex aggression (see Krems et al., 2015, 2020, 2021). Therefore, the field has many areas for future investigation, and we explore some of these in the following sections in more depth.

State of the Field Currently

Competition needs some form of aggression in order to occur (Schuster, 1983). Here it is useful to consider aggression as any action or behavior that is performed with the goal of harming or irritating another individual (Barron, 1977; Buss & Shackelford, 1997). There are many ways in which individuals can harm others (A. Buss, 1961). The current literature tends to divide aggression into various modes, most typically direct or indirect aggression. Direct aggression generally refers to face-to-face conflict, whereas indirect aggression specifically refers to attempts by a perpetrator to cause harm while simultaneously attempting to appear as though there is no harmful intention (Björkqvist et al., 1992a; Björkqvist et al., 1992b). Indirect aggression may rely on tactics of relational or social aggression (Crick & Grotpeter, 1995; Galen & Underwood, 1997), such as the manipulation of peers via their relations and reputation as well as interference with friendships, social inclusion, and group composition. Thus, most work considers indirect aggression to include tarnishing a rival's reputation or excluding them from a group. Further, the aggressor can claim that the acts were not performed for aggressive purposes, or even disguise their identity or diffuse responsibility for the act to the entire group, theoretically mitigating the likelihood that targets of aggression retaliate against indirect aggressors.

In all, girls and women typically use a variety of nonphysical aggressive tactics: they criticize others' clothing, appearance, or personality, they try to win over others to their side; they ostracize rivals from the group; and they spread negative, damaging gossip (Benenson, 2014; Campbell, 2002; Björkqvist, 1994; Owens et al., 2000; Reynolds, 2021; Simmons, 2002). Often, the aggressive acts are performed from within a group, which intensifies the effect on the target because they perceive more aggressors as being involved (Simmons, 2002; see also Hess & Hagen, 2019). A link between indirect aggression and puberty has

been documented, as earlier onset in sexual behavior has been documented in aggressive girls (White et al., 2010). Recent longitudinal work further suggests that those who employ indirect aggression in youth continue to do so in adulthood (Vaillancourt & Farrell, 2021).

Mating Competition Overview

As we have stated in the previous section, much of the work on female–female competition has understandably focused on women's competition for access to and retention of desirable mates. As with men's intrasexual competition for mates, women's mating competition often revolves around competing with same-sex others to display those characteristics most desired by men (self-promotion) and to prevent rival women from being seen as possessing those characteristics (competitor derogation). Unlike much male–male competition for mates, however, most female–female competition for mates is enacted nonphysically and via often subtle and/or covert tactics.

A first question might be what are women competing for, or, relatedly, why should women compete for mates at all? Within the realm of mating, women compete to gain access to mates who are of high quality, as observed by men's kindness, intelligence, physical attractiveness, parenting qualities, and ability to accrue resources, among other factors. Physical attractiveness may be preferred for several reasons, such as its link to qualities cuing likelihood of competitive success (e.g., for resources) and associated status, to ability to protect partners (as well as offspring, kin, and other allies), and/or to "good genes" (i.e., underlying genetic quality and the associated ability to resist environmental pathogens) (e.g., Cantu, 2003; Dixson et al., 2010; Puts, 2010; Windhager et al., 2011). Other male features, such as averageness, also matter given that it indicates the presence of "normal" nondeleterious genes as compared with the surrounding population, as would otherwise be evidenced by mutations or other potential impairments (Langlois & Roggman, 1990). Additionally, sexually dimorphic traits reliant on testosterone levels may also be used to gauge attractiveness—or dominance (Windhager et al., 2011)—and may serve as a proxy for men's ability to gain social status and, consequently, be strong providers of resources (e.g., Thornhill & Gangestad, 2008). Parenting and related provisioning are also highly prized by women. Gray and Anderson (2015) outline the variance in men's parenting, and how the ability and interest in providing care influences the survival of their children (LaCerra, 1994; see also Scelza et al., 2020). Men are also highly variable with respect to their ownership of resources, which is important because, historically, women have

been less able to amass resources independently. Resources may play a crucial role in the ability to provide sufficiently for the woman and any children (see Fisher, 2013, for a review), thereby significantly impacting on women's fitness outcomes and giving rise to women's preference for resource-rich men (Kaplan, 1994; Symons, 1979). In sum, men with these qualities are expected to be deemed more desirable; by virtue of this variance, women are more likely to compete for access to these men. If the local mating market contains a lack of quality mates, competition for desirable mates should increase (Dillon et al., 2017).

Like men, women compete with one another in the currency of the other sex's mate preferences. In addition to the top characteristics shared by both sexes in selecting prospective mates (e.g., kindness and intelligence), men additionally prefer female mates who are young and physically attractive, which can cue future reproductive potential crucial to men's fitness outcomes; for long-term mates, men additionally prefer women who are likely to be sexually faithful (due to issues of paternity uncertainty; Buss, 1988, 1989; Buss & Schmitt, 1993; Kenrick & Keefe, 1992; Kenrick et al., 1996; Symons, 1995, 1989). Given these preferences, much of women's mating competition quite sensibly revolves around wanting men to view them as physically attractive and faithful while also denigrating other women's attractiveness and reputations for fidelity (Reynolds et al., 2018; Vaillancourt, 2013). Women's competition over appearing attractive exists across cultures, but it may be enhanced in Western nations wherein women are bombarded with advertisements for skin care, hair care, age-defying makeup, shapewear and clothing that accentuate a woman's waist, high heels that accentuate a woman's lumbar curvature, and so on; these products act on evolved cues of female future reproductive output. These features, along with many other self-perceptions about one's personality, parenting potential, and so on, compose one's sense of mate value, which in turn is used to measure potential rivals in comparison to oneself. Further, though, women must think about the mate value of potential rivals in terms of their attractiveness (and other preferred characteristics) and evaluate their probability of winning a competition for a desired mate (Fisher & Fernández, 2017).

Thus, perhaps more informative than women's self-promotional competition is women's competitor derogation. For example, Buss and Dedden (1990) find that, compared to men, women were more likely to say that their same-sex rivals were sexually promiscuous, which can effectively preclude those targets from enjoying the benefits of long-term mateships with men (Buss & Schmitt, 1993). Moreover, this sort of derogation is thought to be spurred by jealousy toward potentially more physically attractive same-sex others (e.g., Owens et al., 2000;

see also Arnocky et al., 2012). Additionally, women who are frequently targeted for same-sex aggression tend to have characteristics that render them strong competitors for desirable mates. For example, more physically attractive women are disproportionately targeted for aggression from other women (Arnocky et al. 2012; Krems et al., 2020; Leenaars et al., 2008). In one study on adolescent females and males, attractiveness increased females' odds on incurring same-sex aggression by 35 percent and decreased males' by 25 percent (Leenaars et al., 2008).

Why Indirect Aggression and How Is It Deployed?

As noted above, an abundance of evidence suggests that women do compete for mates. Here, we discuss the current understanding on how women go about doing so; indeed, perhaps the greatest strides on understanding women's intrasexual competition have been made due to examinations of their preferred mode of competition. For both sexes, aggression can be a tool capable of solving multiple adaptive problems (Buss & Shackelford, 1997). Whereas men tend to use physical and directly aggressive acts in their same-sex competition, work from Burbank (1987), Crick and Grotpeter (1995), Björkqvist (1994), and Campbell (2002), among others, strongly suggest that women prefer to use nonphysical forms of aggression that may be considered indirectly oriented when competing intrasexually (see also Vaillancourt, 2013).

INDIRECT AGGRESSION TACTICS

These indirect tactics include gossip, derogation, and social exclusion, but it is important to realize that this class of tactics has been variously titled (see Archer & Coyne, 2005; Hess & Hagen, 2006, 2019). For example, Björkqvist et al. (1992b, p. 52) defined *indirect aggression* as "a kind of social manipulation: the aggressor manipulates others to attack the victim, or, by other means, makes use of the social structure in order to harm the target person, without being personally involved in the attack. Thereby, the aggressor stands a greater chance of going unnoticed and avoiding retaliation." Grotpeter and Crick (1995, p. 711) defined *relational aggression* as including "behaviors that inflict harm on others by manipulating their peer relationships (e.g., by giving a peer the silent treatment, maliciously spreading lies and rumors about a peer to damage the peer's group status)" which they viewed as more characteristic of girls than boys. Galen and Underwood (1997) defined *social aggression* as being directed toward damaging another's self-esteem, social status, or both and may take direct forms such as verbal rejection, negative facial expressions or body

movements, or more indirect forms such as slanderous rumors or social exclusion.

Why do women compete using these various nonphysical, often subtle tactics? Answers to this question typically revolve around the effectiveness of these tactics for women in that the tactics minimize harm to aggressors (e.g., via revenge from victims or third-party retaliation) while perhaps simultaneously harming rivals in arenas that are uniquely impactful.

First, some have theorized that the costs of engaging in physical aggression are too costly for females. For example, according to Björkqvist (1994), women have developed alternative strategies to effectively compete because they have lower physical strength compared to men. (Although note that this argument has received challenge in the case of female intrasexual competition, where competitors would be fairly equally matched; e.g., Fessler et al., 2004).

Indirect tactics are themselves not only nonphysical and often not enacted face to face, but they may be less likely to incur revenge from the target of third-party punishment. The theorized importance for women's avoidance of physical retaliation and revenge has been clearly laid out by Campbell (1999). On this view, staying alive and reducing the potential for harm is a successfully developed adaptation in women to promote reproductive success because it is more critical that mothers remain alive than fathers, particularly in terms of reducing infant mortality (see for support Sear & Mace, 2008). The selective pressure of child mortality warrants attention: prior to modern history, infant mortality rates ranged from 25 percent to 40 percent, and child mortality rates from 36 percent to 50 percent, which echo modern hunter-gatherer groups (23 percent and 46 percent, for infant and child mortality, respectively) (Volk & Atkinson, 2008). Mothers are typically the primary caregivers and protectors of children, and maternal death greatly impacts on infant and child mortality (at least to age two; Sear & Mace, 2008). Hence, Campbell (1999) argues that the greater importance of the maternal presence rendered potentially lethal physical aggression too costly a gamble, leading to women's preference for less physical tactics of aggression. Competition for status is generally avoided, and instead competition circles around access to limited resources, using indirectly aggressive strategies (but see Benenson, 1999; Liesen, 2013). Moreover, physical tactics do not necessarily benefit female aggressors, even as they might more obviously and greatly harm victims; for example, whereas women might be attracted to male victors of physical contests, men are not equally attracted to female victors (see, e.g., Benenson & Abdazi, 2020).

Second, women's aggression is typically aimed at harming victims' reputations and, relatedly, their social relationships (Buss & Dedden, 1990;

Reynolds et al., 2018). These may be especially dangerous targets for female victims. For example, denigrating the reputation of a female rival by calling her sexually promiscuous employs rumor-spreading that can impact on that victim's ability to form long-term relationships with male mates (Buss & Schmitt, 1993; Hess & Hagen, 2019). Moreover, compared to a rumor about a man (e.g., he is poor), this rumor about sexual promiscuity is difficult to refute, making it rather effective (see Hess & Hagen, 2019). We return to the effectiveness of these tactics for harming female targets shortly.

Notably, Liesen (2013) holds a somewhat different perspective, particularly with regard to Campbell's (1999) account for women's preference for indirect aggression. Liesen (2013) contends that girls and women rely on strategies to pursue status and dominance in order not only to access material resources but also establish alliances and reduce the potential for harassment (see also Benenson, 1999; Hess & Hagen, 2006). This view means that the goal is not to be at the top of the hierarchy but to be near the center of activities and social networks where there is the best probability of receiving benefits. These ideas are echoed in women's "tend and befriend" response (Taylor et al., 2000) to stressful situations, which they are argued to use instead of a fight-or-flight response. Tending here refers to caring for children and blending into the environment, whereas befriending is the creation of social networks of people who may provide resources and protection for her and her children. However, although women's intrasexual competition for friends is somewhat well documented in ethnographic and sociological work (e.g., Owens et al., 2000; Simmons, 2002), it is not well studied empirically.

Also holding a slightly different view of women's competition is Benenson (2014), who makes a strong case that social exclusion of same-sex others is a type of aggression especially well tailored to harm female victims and benefit female aggressors. Although social exclusion *can* be nonphysical, occur "behind-the-back," and/or be subtle, this type of aggression may not fit well under the umbrella of indirect aggression, as it can and sometimes does include physical elements, occur "face-to-face," and be quite overt. There is strong evidence that women are more likely to exclude same-sex others as compared to men, but why? Benenson (2014; Benenson et al., 2011, 2013) focuses on sex differences in social ecology in providing a cost-benefit analysis of social exclusion for women versus men. She suggests that compared to men, women have both less to lose from excluding a same-sex other from the group and likely more to gain from doing so. That is, whereas men band together in intergroup conflicts—a numbers game in which every member counts—women do not, nor would another woman in the group necessarily help in that group's defense. As a

result, the loss of a single same-sex other might be less costly in women's minds than men's minds. Similarly, including a female newcomer who might diminish the group's finite resources could have more negative consequences for females and their offspring, whereas excluding another female might increase females' access to more and preferable resources. By contrast, for men, including a male newcomer might bolster their chances of winning intergroup conflicts, and excluding that male might likewise decrease their chances of doing so.

EFFECTIVENESS AND OUTCOMES OF INDIRECT TACTICS

Another way to answer the question of why women typically aggress against other women via what we refer to as, collectively, indirect tactics is because these tactics are particularly effective—that is, they are potentially high impact *and* low cost. Considering this question, Vaillancourt (2013) notes two major swaths of evidence for the success of women's indirect aggression against other women: first, it can eliminate competitors by reducing those competitors' desire to compete for mates. Related, and not mutually exclusive, women's indirect aggression might also decrease victims' abilities to effectively compete for mates. For example, when an attractive woman derogates another woman's appearance, this act can lead the target to suffer lower esteem in the eyes of men (Fisher & Cox, 2009), making her a weaker rival for men's affections. Moreover, indirect victimization from same-sex peers may be correlated with a host of negative consequences; women (and girls) may experience these negative consequences more acutely than men (and boys; see Vaillancourt, 2013). For example, any amount of indirect peer victimization was associated with girls' suicide attempts, whereas only frequent indirect peer victimization was associated with boys' suicide attempts (Klomek et al., 2008). Finally, nonhuman animal evidence suggests that harassment from other females can impact on victims' physiology in such a way that inhibits their reproductive potentials (e.g., preventing ovulation; Stockley & Bro-Jørgensen, 2011), although more research is needed to elucidate whether and by which mechanisms this might occur among humans. One possibility is that harassment leads victims to experience stress and consequently lose weight, ultimately leading to reproductive suppression through anovulation (Salmon & Crawford, 2012).

Another line of evidence for the effectiveness of women's indirect aggression against other women comes from work on adolescents, implying that those females who aggress more frequently enjoy better mating outcomes. For example, girls using indirect aggression frequently may begin to date earlier than their aggressed-against peers and be more popular dating partners than those peers (see Vaillancourt, 2013; Vaillancourt & Krems, 2018). Thus, just as

indirect *aggressors* may avoid the costs of (and benefits, when applicable) being revealed as an aggressor—which may be more beneficial for women—some evidence also suggests *victims* of indirect aggression may suffer more than male victims.

Mating vs. Other Arenas

Fitness is often called the "coin of the realm" in evolutionary social science, and there is a clear, obvious line between securing a desirable mate and women's fitness; thus, it is not surprising that researchers would focus first on women's competition for desirable mates. At the same time, it is also important to acknowledge that this focus has been, to some extent, to the exclusion of others forms of women's competition. In doing so, we can identify some nascent areas of study relating to female intrasexual competition that have been relatively ignored or overlooked by previous scientists. Whereas these move beyond mating, strictly speaking, many of these areas are nevertheless tightly linked to women's fitness outcomes.

Most closely linked to the work on women's same-sex aggression in the course of mating competition is a trend to explore women's defenses against this aggression. This work begins from the premise that women's preferred tactics of same-sex aggression present challenges that may be somewhat distinct from those faced by men's mating competition. For example, Krems et al. (2015) reasoned that although women are just as likely to get angry and enact intrasexual aggression as are men, women often hide that anger and aggress indirectly, implying that women's victims face a challenge in anticipating another woman's anger and anger-based aggression. One means for mitigating the threat of other women's aggression, then, might be to overperceive other women's genuinely neutral faces as seeming angry, perhaps allowing female targets to engage in strategies to allay the angry women's emotions or gather defenders in advance of incoming aggression. Notably, those women who face disproportionately high levels of same-sex aggression—most often physically attractive women—exhibited the greatest tendency to misperceive women' neutral faces as being angry. In this same vein, other work has identified the specific challenges women face as targets of intrasexual aggression and endeavored to test whether women might possess defenses against these recurrent threats (e.g., Krems et al., 2020; Krems et al., 2021). However, this work remains largely in its infancy, with much more to be done.

Also building on foundations of existing intrasexual mating competition work is another understudied area: single mothers as potential rivals for mates. One

proposition is that mothers have an advantage over single, nulliparous women because the former have proven their ability to conceive and bear children. All else equal, men might prefer single mothers due to their inarguable fecundity. Single mothers might also have an advantage over partnered mothers insofar as the latter possess male mates, who can represent significant mating competition. The proposal of single mothers as mating rivals is interesting because traditional theory holds that mothers should be viewed as allocating their investment to parenting rather than reproduction but a review of single parents by Gray and Garcia (2013) suggests otherwise. Fisher et al. (2019) found that single women were less positive in their attitudes and beliefs about single mothers than partnered women, and viewed single mothers as potential mating rivals. Further, those with a history of manipulating rivals in mating situations, such as deceiving rivals by providing false information, were significantly more likely to have knowingly competed with single mothers for mates.

Other work has endeavored to push past the strong emphasis on mating competition to explore competition for other resources, but we know far less about this type of competition. For example, mothers' competition to secure resources, women's competition over best friends, and women's status competition remain very understudied. Moreover, evidence suggests that these resources might have nonnegligible impacts on women's fitness outcomes, and thus suggest that we should expect women to engage in intrasexual competition for access to those resources (see, e.g., Cassar & Rigdon, 2021; Krems et al., 2022a, 2022b).

In terms of women's competition in relation to mothering, there have been theoretical reviews of how mothers must cooperate *and* compete, exhibiting the same flexibility that was mentioned at the start of this chapter (Fisher et al., 2017a; Fisher & Moule, 2013; Sokol-Chang et al., 2017). In terms of cooperation, mothers must create allies to share resources, childcare, and various forms of support, given these directly impinge upon both a mother's own and her child's survival (Hrdy, 2009). For example, it is possible that women may engage in synchronous (yet unplanned) pregnancies with friends, and plan to maximize sharing of resources, knowledge, and childcare (Worth & Fisher, 2011). Anecdotal evidence further suggests the reallocation of new mothers' finite time and energy to attracting and remaining friends with fellow mothers—potentially increasing benefits from other mothers' knowledge—but at the cost of attracting and retaining child-free friends. In terms of competition, the occurrence of maternal competition remains understudied. For example, to date the only article on maternal competition in humans is Linney et al. (2017), who document self-reported maternal attachment as well as various responses to a

situation where a mother is making a point that she is a better mother than oneself, among other issues.

Throughout our evolutionary history, it is likely that (1) mating competition did not stop at a women's successful reproduction (i.e., becoming a biological mother), and (2) mothers engage in competitive strategies such as self-promotion and competitor derogation particularly with other women at a similar life stage who are competing over the same resources (i.e., other mothers). For example, in naturally fertile populations, such as the Dogon, women overlap for the majority of their reproductive windows which suggests that competing with other mothers would have been a constant situation (Strassman, 1992). Although mother–mother competition is understudied, one way to test this behavior in a modern Western setting is to use social media posts where mothers advertise themselves or their children to a social network. Using this method, Benoit and Fisher (2019) documented that mothers who derogated other mothers' competencies, personality, and appearance were viewed negatively by others, and far more so than mothers who self-promoted on the same characteristics. Most important, those making the statements were viewed to be less competent as mothers themselves. However, mothers who promoted their maternal competencies were perceived to be less likable compared with baseline ratings, but all other ratings remained stable (e.g., her maternal competency, kindness, trustworthiness, intelligence, attractiveness, loyalty, and friendliness). Related, one may speculate that mothers might additionally compete via touting the success of one's offspring (e.g., "Alex is going to Oxford!" and "Tabby is marrying a doctor"), and therefore one's own parenting skills. Indeed, insofar as they are perceived to be the primary caretakers of offspring, such indirect advertisement might yield a reputational boost to mothers in particular (relative to fathers). At the same time, denigrating another person's child might have more negative reputational consequences for that child's mother (vs. father).

Other work has begun to explore possible competition for friends. Sustained close friendships can benefit female fitness outcomes in numerous ways. These fitness consequences of having a few close same-sex friends are perhaps best illustrated in work on female baboons; having a few close female friends may increase female baboons' survivability and that of their offspring (e.g., Silk et al., 2003). The presence of friends might additionally buffer one from social exclusion and its negative costs, and female friends can also serve as both alloparents and effective co-aggressors (Hess & Hagen, 2006, 2019, 2022; Hrdy, 1999). Other work, particularly in the nonhuman primate literature, suggests that female friendships can buffer females against male harassment and control (e.g., Campbell, 2002; Setchel et al., 2006; Smuts & Smuts, 1993; Tokuyama Furuichi,

2016; but see Benenson, 2014). Thus, one might expect women to be perhaps even more competitive than men when it comes to attracting and retaining one or two best and close friends. Indeed, qualitative work and observations from developmental psychology and sociology suggest that girls' and women's competition for friends can be most ferocious (e.g., Owens et al., 2000; Simmons, 2002).

This is not to say that men's friendships are less important to men than women's are to women. Rather, among humans, structural differences in men's and women's friendships may render the loss of women's close friends especially costly (Benenson, 2014; Krems et al., 2022a). Whereas men form loose multimate group friendships, women typically form one or two very close friendships, which are time-intensive and full of self-disclosure—information that could be used against a woman in the event the friendship ends. This closeness suggests that women might be especially jealous at the formation of rival friendships, which is evidenced in existing developmental and experimental work (Krems et al., 2021, 2022a; Parker et al., 2005), and supports this notion that women may be especially competitive in retaining close friends. (By contrast, men reported greater friendship jealousy when acquaintances made new friends, perhaps reflecting the importance of having more supporters in group-based conflicts; Krems et al., 2022a)

Women's competition for status is a fascinating area with many recent developments. Traditionally, much work on status and related status competition has overlooked women, perhaps because theory expected status competition to be more beneficial for men (see, e.g., Campbell, 1999). Another reason for the comparative dearth of work on women's status may again be related to women's tactics of competition; that is, they may be less easy to observe (perhaps by design). However, more recent work is starting to push back against the idea that women are not interested in status and, instead, are engaging in competition for status. For example, Cassar et al. (2016) challenge this notion by showing that giving women the ability to compete on behalf of others and allowing women the option to cooperate decreased the sex/gender gap in competition for resources. Work in the related domain of leadership by Hagen and Garfield (2019; Garfield et al., 2019) suggests some tantalizing future directions as well, picking up the torch from earlier work by evolutionary anthropologists (e.g., Low, 1990, 1992, 2005; Whyte, 1978; Yanca & Low, 2004). Perhaps even more fundamentally, Buss et al. (2020) are now challenging the long-held conceptualizations of status as being the same for men and women (see also Krems et al., 2022b). Their work explores sex differences in instantiations of status across fourteen nations, finding, for example, that beauty is a more

important status criterion for women than for men. This implies that existing definitions of status in psychology might be guilty of hewing too close to the male-biased defaults (see Benenson, 1999). When most people think of status, they might think about physical formidability or great wealth, but these features might be more apt instantiations of men's than women's status. If we agree that women have faced sex-specific challenges, perhaps especially in the course of navigating and achieving influence within their same-sex social circles, then perhaps we should expect that women's status might rely on more distinct criteria than men's.

Future Directions

An area that warrants attention in the future is how women intrasexually compete in non-WEIRD (i.e., Western, educated, industrial, rich, and democratic; Henrich et al., 2010) cultures. In their work with the Tsimane and how reputations are linked with intrasexual competition, Rucas et al. (2006) point out that small-scale societies are particularly important to study, given that the formation of reputations and the sensitivity to reputation effects are highly salient due to lifelong recurring interactions between individuals. The Tsimane produce their own food directly, or access it indirectly via sharing in their social networks. Women's reproductive success is limited by access to resources, and cooperation among women (as well as among men, and among men and women) is vital to their fitness. There is continuous competition for resources—social resources such as alliances as well as information and more tangible resources (e.g., meat), which women might typically access via their relationships. Further, there have been numerous related ideas in past research that deserve attention. For example, Burbank (1987) documents how cowives in polygynous societies intrasexually compete for food and money, paternal care for their children, and for their children's inheritance, and yet these behaviors have remained understudied.

There is also a need to examine women's intrasexual competition among women who do not consider themselves exclusively or primarily heterosexual. The study of women's sexual fluidity has gained substantial momentum among evolutionary-informed researchers (for a review, see Fisher et al., 2021). However, how fluidity relates to competition among women remains unexplored. Further, how does one both cooperate and compete for same-sex mates, given that a competitor may herself be considered at a later date to be a prospective mate? Initial findings suggest that lesbian and straight women compete in very similar ways for mates; both groups use competitor derogation

and are more likely to target women they perceive to be sexual threats (Hughes et al., 2020). There remain many avenues for further study.

Another relevant topic that has been almost completely ignored by academics is so-called mommy judging, which here we define as the way that mothers feel, or are, scrutinized for decisions related to their mothering. Preliminary qualitative research into competition between mothers quickly led to the study of how mothers are evaluated by others, with the expectation that the areas in which mothers feel judged would be those that are used in competition against each other, and against other women in general (Daley & Fisher, 2016). The findings reveal that nonmothers judge mothers less severely than mothers, and that children are often used as a vehicle by which one's competency as a mother is assessed. Mothers who represent potential mating rivals (i.e., youthful, fit mothers) are judged the most harshly; however, these data remain preliminary thus far (Fisher, 2017a).

Another area of interest is competition among women who are postreproductive (or postmenopausal). While postreproductively aged women may be an evolutionary novelty, over the past century it is not uncommon in Western cultures to spend 30 percent to 40 percent of their lives in this state (Lumsden & Sassarini, 2019). Women of all ages benefit from having close alliances, and therefore, the competition for friendship detailed in the previous section may be critically important among postmenopausal women. Aside from the emotional and cognitive benefits of friendship among elderly women, friendship is very strongly correlated with reduced (pre)frailty (Uno et al., 2021), presumably because friends lead for greater physical activity and stronger participation in sociality. Given the advantages of having close friends, it is sensible to predict that postmenopausal women may compete to attain and retain friends. This prediction has gained support through a survey of elderly women, where it was found that hypothetical vignettes concerning the "theft" of a friend led to a reported increase in competitive tactics to win back the friend (Fisher et al., 2019).

There has been an explosion of research on women's intrasexual competition. While mating competition has remained the primary focus, the ways in which researchers have explored mating-relevant behavior has expanded considerably. For example, how parents and daughters have conflicting interests in the latter's mate selection criteria has been examined (Kennair & Biegler, 2017; Perilloux et al., 2008), as has the influence of environment via operational sex ratios (Dillon et al., 2017), how competition varies across the lifespan according to fluctuating hormonal profiles (Cobey & Hahn, 2017), and the influence of ovulatory hormones and fecundity (Nikiforidis et al., 2017), to name just a few. Within

each of these topics, many areas remain to be studied. Thus, whereas the focus on intrasexual competition for the purpose of mating is sensible, as we discussed, it is interesting to see how the area has so greatly expanded in scope and will continue to do so over time.

It will also be interesting to see how future researchers examine their daily events in light of the existing research on competition. Take, for example, "Operation Varsity Blues," which was the name for the scandal over college and university admissions in the United States that hit the media in 2019. Famous celebrity parents and other wealthy individuals paid for a college counseling and preparation service which was known to lead to admission to high-ranking colleges and universities. This service, primarily run by William Singer, relied on bribed standardized test proctors who altered test answers after the exam was submitted. He also bribed coaches to falsely certify students had been recruited to teams (Greenspan, 2019). Here mothers, including actresses Felicity Huffman and Lori Loughlin, paid large sums of money to have their daughters granted access to college. Huffman paid approximately $15,000 to have Singer modify test scores, whereas Loughlin paid an estimated $500,000 to have her two daughters gain admittance to the University of Southern California (Breuninger, 2019). These affluent mothers were clearly competing by using their monetary resources to advance their daughters' careers, which would invariably help position them to secure higher-quality mates. Current events such as this scandal provide naturally occurring evidence of women's competition in ways that truly matter to them, such as to promote their children's social standing, to promote their children's likelihood of independently acquiring resources, and to ensure that their children establish successful mating relationships.

Conclusion

Hrdy (1999) called researchers to examine topics that were important to women, in order to be able to address how they compete, why they compete, and the benefits and costs associated with their competition. She argued that the traditional model of same-sex competition for hierarchical status did not meaningfully apply to women. In the years following her call, the field has grown to a remarkable degree. The subtlety of women's decision-making regarding when (and with whom) to cooperate versus compete is starting to come to the forefront. How women defend themselves from same-sex aggressors and the role of friendships is now part of the growing body of scientific knowledge. No longer is the literature strictly connected to women's competition to acquire desirable mates—while informative and highly relevant, women's

lives do not end with mating, and neither does their intrasexual competition.

Some readers will find value in our review of how the topic has grown over time and the corpus of work that has been performed thus far. Potentially there will be opportunities in the coming decades to use this review as a stepping-stone to show how the area has changed yet again, or how it has expanded or narrowed due to the accumulation of discoveries. With time, we predict that studies will become increasingly focused on capturing the nuances of women's competition, stressing their covert and subtle nature, and will further explore the complexities of women's decision-making in terms of maintaining strong social alliances and yet moving into central positions of power (e.g., Liesen, 2013). We review how women's aggression tactics, and particularly indirect aggression, are tied to competitive strategies, and how they are thought to decrease the potential for physical harm (Campbell, 2002). Intimately connected to these ideas is the critical importance of mothers for infant and child survival, and how women must strategize to reduce physical risk and maximize safety during competitive interactions. Our review points out, though, that women do care about status (Cassar & Rigdon, 2020), so the challenge to determine how women configure social status, use status to help others, and compete for status remains.

Our review clearly shows the need for maintaining a phylogenetic approach; although we do not deeply discuss the nonhuman primate findings that apply to female competition, we have highlighted the inclusion of such work. We acknowledge the strength and necessity in including results from the nonhuman primate literature in the development of models and theory.

Much of our review pertains to the topic of women's intrasexual competition in relation to mating. The preponderance of such research is to be expected, given that the consequences of mating are so important or weighty for women, due to obligate parental investment (Trivers, 1972). However, the focus on mating-themed research has overshadowed other ways that women compete that presumably heavily influence fitness. We discuss competition among mothers, for example, as well as how women defend themselves against intrasexual aggression. We encourage scholars to examine other topics that are more indirectly tied to mating, but also topics that influence fitness in other ways. We present some potential topics in our discussion of future directions in the hopes of inspiring new lines of questioning that will allow the area of female intrasexual competition to continue to grow.

In sum, girls and women may appear to be made of sugar and spice and all things nice. However, such social perceptions can at once reflect females' genuine cooperation as well as deeply rational means for navigating their social worlds—securing high-quality mates and allies while avoiding the costly

retaliation from appearing to compete for those same resources. Females must intrasexually compete but remain flexible enough to cooperate, all for purposes of increasing their individual fitness. The degree of this flexibility is slowly being revealed through increased research and will continue to expand over the coming decades.

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CHAPTER
15

Mate Competition *between* the Sexes: Evidence from Two Non-Western Cultures

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Abstract

Darwinian sexual selection has been the dominant framework for understanding mate competition, which usually involves intrasexual competition for opposite-sex partners. This expected dynamic can become more complicated in any species that shows an appreciable rate of bisexual behavior. Specifically, *intersexual* mate competition is possible any time opposite-sex individuals engage in romantic/sexual competition over the same target. We review historical and ethnographic evidence that intersexual mate competition occurs among humans. Going further, we describe data from two different non-Western cultures—Samoa and the Istmo Zapotec (Oaxaca, Mexico). These data show that competitions to acquire and maintain sexual relationships with men occur between women and feminine same-sex attracted males. This intersexual mate competition most commonly involved feminine males attempting to mate-poach partnered men from their relationships with women. Using participant stories to complement mixed-methods data, we illustrate how these competitions typically involved feminine males attempting to entice the target man, whereas women engaged in mate-guarding and emotionally punitive behaviors. Although intersexual mate competition is unlikely to be found in most species, or across all human cultures, our data show that intersexual mate competition can ensue when males and females prefer the same sexual partners, who themselves behave in a bisexual manner.

Key Words: sexual selection, intersexual competition, cross-cultural research, male androphilia, mate competition tactics, mate poaching, mate retention

Mrs. Madrigal: "*The town is full of charming young men.*"
Mary Ann Singleton: "*To each other*."
Mrs. Madrigal: "*Take it as a challenge. When a woman triumphs in this town, she<u>really</u>triumphs*."

—The landlady, Mrs. Madrigal, consoling her tenant, Mary Ann Singleton, about the complicated realities of the 1976 San Francisco mating market in Armistead Maupin's (1978) Tales of the City.

Sexual Selection and Mate Competition

Sexual selection is the key theoretical framework for understanding sexual behavior from an evolutionary perspective. It depends on the advantages certain individuals have over other individuals in relation to reproduction (Darwin, 1871). How the sexual selection process occurs has been overwhelmingly conceptualized in terms of two interactive mechanisms: intrasexual competition among males for female reproductive partners and choice of male reproductive partners by females.

Given that evolution via sexual selection is contingent on reproduction, one of the most basic tenets of sexual selection theory is that individuals should behave in ways to maximize their reproductive success. It should therefore come as no surprise that evolutionary psychologists have overwhelmingly examined human mating psychology as if reproductive interactions were hermetically sealed off from nonreproductive ones (e.g., Buss, 2013; Campbell, 2013; Davies & Shackelford, 2015; Schmitt, 2014). This approach, although understandable, does not reflect a more complex (and interesting) reality; namely, reproductive and nonreproductive sex develop and evolve in concert, and each can influence the other (Bailey & Zuk, 2009; Vasey, 2006; Vasey et al., 2014a).

By way of illustrating this point, we review some of our research on *inter*sexual mate competition for masculine male sexual partners between women and same-sex attracted males. This work draws on data collected in two distinct cultures—Samoa and among the Istmo Zapotec of Oaxaca, Mexico. Both of these cultures are considered to be independent from each other in terms of cultural diffusion or common cultural derivation (Murdock & White, 1969). Our work on this topic shifts focus from purely functional questions about *why* same-sex sexuality exists—questions that dominate the literature—to understanding the evolutionary *consequences* of same-sex sexuality for heterosexual mating systems as a whole.

Same-Sex Oriented Males in Cross-Cultural Perspective

Before discussing our work on intersexual mate competition, it is important to understand that any attempt to undertake comparative cross-cultural research on male sexual orientation must focus on the *deep structure* of sexual orientation that transcends differences related to how male same-sex sexual orientation is expressed, and conceptualized, within culturally specific contexts. The deep structure of male same-sex sexual orientation can be thought of as a set of traits that characterize same-sex attracted males regardless of the cultural context in which they are found. A focus on *sexual feelings* that are context-independent facilitates cross-cultural comparisons (Brown, 1991) in a manner that culturally specific identity categories do not. To this end, the use of some specialized language is required. *Androphilia* refers to sexual attraction and arousal to adult males, whereas *gynephilia* refers to sexual attraction and arousal to adult females (Blanchard, 1985).

The manner in which male androphilia is publicly expressed varies cross-culturally but takes on two primary forms (Murray, 2000; Nanda, 2014). In Western societies, the most common form of male androphilia is the cisgender one (e.g., "gay men"). *Cisgender androphilic males* behave in a *relatively* masculine manner and, in Western societies, they are typically identified as "men" by themselves and others.

In contrast, in many non-Western societies, the most common form of male androphilia is the *transgender* one. *Transgender androphilic males* typically behave in a highly effeminate manner, and in many non-Western cultures they are identified by themselves and others as members of a nonbinary gender, differentiating them from both "men" and "women" (Nanda, 2014).[1] Examples include, but are by no means limited to, the *fa'afafine* of Samoa (Vasey & VanderLaan, 2016) and the Istmo Zapotec *muxes* of Mexico (Mirandé, 2017).

Although cisgender and transgender androphilic males differ in many dramatic ways from each other, in terms of the deep structure of sexual orientation both can be accurately described as "androphilic biological males." Nearly two decades of comparative cross-cultural research indicates that both cisgender and transgender male androphiles share numerous biodemographic, psychodevelopmental, and cognitive-behavioral correlates. Compared to gynephilic males, both forms tend to have a greater number of older biological brothers (e.g., Blanchard, 2018; Gómez Jiménez et al., 2020b; Semenyna et al., 2017a; VanderLaan et al., 2016), more androphilic male relatives (e.g., Gómez Jiménez et al., 2018; Schwartz et al, 2010; Semenyna et al., 2017b), similar population prevalence rates of ~2–6 percent of males (e.g., Gates, 2011; Gómez

Jiménez et al., 2018; Semenyna et al., 2017b), little or no offspring production (e.g., Coome et al., 2020; Schwartz et al., 2010; Vasey et al., 2014b), elevated cross-sex beliefs and fantasies in childhood (e.g., "I wish I was a girl") (e.g., Bailey & Zucker, 1995; Vasey & Bartlett, 2007), more childhood sex-atypical behavior (e.g., Bailey & Zucker, 1995; Bartlett & Vasey, 2006; Gómez Jiménez et al., 2020a; Petterson et al., 2017), elevated childhood separation anxiety (e.g., Gómez et al., 2017; VanderLaan et al., 2011; Vasey et al., 2011), a preference for female-typical occupations (e.g., Semenyna & Vasey, 2016; Zheng et al., 2011), and similar genital arousal (Chivers et al., 2007; Lawrence et al., 2005) and viewing time patterns (Petterson et al., 2018) when presented with images of men and women. Taken together, this body of research suggests that both cisgender and transgender male androphilia represent cultural variants of the same trait, and thus share a common biological origin.

Relationship Formation by Androphilic Males in Cross-Cultural Perspective

Although androphilic males are, by definition, sexually attracted to adult males, they commonly express sexual interest in *masculine* adult males (regardless of the masculine adult males' sexual orientation) and sexual aversion toward *feminine* adult males (Bailey et al., 1994; Petterson et al., 2018). Sexual attraction to masculine males and sexual aversion to femininity can be considered part of the deep structure of male androphilia. Although this pattern of sexual psychology is shared by both cisgender and transgender male androphiles, it motivates them to form different types of relationships, which can range from fleeting sexual encounters to multiyear partnerships.

It is not uncommon for cisgender androphilic males to be sexually attracted to cisgender gynephilic males, but this interest rarely, if ever, results in sexual activity because the latter are not interested in masculine sexual partners. Consequently, cisgender androphilic males routinely engage in sexual activity, and form romantic relationships, with other cisgender androphilic males because such partners are relatively masculine, and unlike cisgender gynephilic males, they are sexually and romantically interested in other cisgender males. These relationships have been described as *homogendered* and *egalitarian* because they involve two individuals who occupy the same gender category (typically, both individuals identify as *men*), do not differ appreciably with respect to age, and treat each other as social equals (Murray, 2000).

In contrast, transgender androphilic males also seek out sexual relationships

with cisgender males, the majority of whom are mostly gynephilic (i.e., Kinsey 1; Kinsey et al., 1948), whereas an appreciable minority are ambiphilic (i.e., sexually attracted and aroused to both adult males and females) (e.g., Petterson et al., 2020; Rosenthal et al., 2017; Stief, 2017; Whitam, 1992). This pattern of relationship formation occurs because cisgender males who are mostly gynephilic or bisexual are interested in feminine sexual partners, whereas cisgender male androphiles usually find them sexually aversive (Bailey et al., 1994; Petterson et al., 2018). These relationships have been described as *heterogendered* or *gender-stratified*, owing to the fact that the cisgender males in question typically identify as *men*, while their transgender partners identify otherwise. Given their gender-differentiated characteristics, the partners often adopt special social roles relative to each other, and consequently, they do not treat each other as social equals (Murray, 2000).

Whitam (1992) has said that gynephilic men's willingness to engage in sexual interactions with feminine biological males who have male-typical genitalia appears to be highly variable across cultures. Indeed, ethnographic research suggests that, in many non-Western cultures, heterogendered sexual interactions of this sort are not uncommon (e.g., Murray, 2000; Nanda, 2014). In contrast, they seem to be relatively rare in the West (Bailey, 2003). The idea that bisexual men might be sexually interested in transgender androphilic males may resonate with many readers, given that such men are sexually attracted to both sexes, and transgender androphilic males possess aspects of both sexes (e.g., feminine gender role presentation and male typical aspects of anatomy). At the same time, it may seem odd to some readers (Western ones, in particular) that a gynephilic male would be sexually interested in transgender male androphiles. After all, gynephilic males—even mostly gynephilic ones—are by definition primarily interested in female sexual partners. It must be remembered, however, that gynephilic men are sexually interested, more globally, in femininity. Not surprisingly then, many men who seek out transgender male androphiles as sexual partners cite the femininity of such individuals as being a key motivator (e.g., Kulick, 1997; Operario et al., 2008; Reback & Larkins, 2006; Rosenthal et al., 2017; Mitsuhashi, 2006). The femininity of transgender androphilic males can often be significantly heightened when compared to the average androphilic woman, creating a supernormal feminine stimulus, which many gynephilic men find extremely attractive (Operario et al., 2008; Reback & Larkins, 2006). In addition, some of these men report that they find transgender male androphiles to be more sexually confident, assertive, skilled, and open-minded when compared to most cisgender women—attributes that they find appealing when expressed by markedly feminine individuals (Operario et al., 2008; Reback &

Larkins, 2006).

Femininity aside, transgender male androphiles who have not undergone breast augmentation and genital reconstructive surgery—the overwhelming majority of such individuals worldwide—possess aspects of male anatomy that gynephilic males typically find sexually unattractive or even sexually aversive. How are these sentiments overcome? In short, many men who seek out transgender androphilic males as sexual partners report that they avoid touching their transgender androphilic male partners' penises altogether to maintain the illusion that their partners are cisgender women (Reback & Larkins, 2006). It seems likely that sexual assertiveness on the part of transgender male androphiles, which can take the form of bold and insistent sexual solicitations, is also important in overcoming any sexual reticence on the part of mostly gynephilic males (Operario et al., 2008; Reback & Larkins, 2006).

Intersexual Mate Competition

With this background on the cross-cultural expressions of male androphilia, we can now turn to a discussion of our research on intersexual mate competition. Women are known to adjust their competitive tactics in response to different degrees of mate competition in the local environment (e.g., Campbell, 2013; Stockley & Campbell, 2013). When same-sex attracted males prefer to engage in sexual activity with masculine men who behave in a bisexual manner, it can create a unique mating problem for androphilic women. In such circumstances, androphilic women not only have to compete with other androphilic women (*intra*sexually) for access to potential reproductive partners as predicted by Darwinian sexual selection theory, but they must do so with same-sex attracted males (*inter*sexually) as well.

Intersexual mate competition occurs when a sexually motivated individual attempts to acquire or maintain exclusive access to a sexual/reproductive partner (the object of competition), while decreasing or preventing an opposite-sex conspecific from doing the same. Two facets of these interactions occur simultaneously; one reproductive and the other nonreproductive. The competitor who is the opposite sex of the focus of competition can be accurately described as the reproductive competitor, whereas the competitor who is the same sex as the object of competition can be accurately described as the nonreproductive competitor. Consequently, how one characterizes these competitive interactions can vary depending on the perspective that is taken: that of the reproductive competitor versus that of the nonreproductive one. Like intrasexual competition for mates, it appears that intersexual mate competition involves behaviors that

could potentially influence the acquisition and retention of reproductive partners through interactions with conspecifics.

Artistic and literary examples of intersexual mate competition abound throughout history. For example, intersexual mate competition is depicted in an anonymously published Japanese picture book from 1675 (*Wakashu-asobi kara no makura*, or *Aloeswood incense pillow of youngman-play*). One panel depicts and describes a woman seducing a *wakashu* (beautiful young male) away from an older man, which is consistent with "several other scenes [that] present men and women as competitors for the affections of *wakashu*, calling the women 'cunning enemies' " (Mostow, 2003, p. 59, and fig. 4.8) who "compete with adult men for the affections of worthy *wakashu*" (Mostow, 2003, p. 60). Irrespective of whether the book captured reality, or depicted fantasy, intersexual mate competition is portrayed as something in which humans are capable of engaging. This example is reminiscent of what Norton (1997) calls a "humorous literature from ancient China to medieval Europe [that is] littered with tales about wives who are anxious or jealous about their husbands' boyfriends" (p. 53). This literary tradition continues into historically recent times as exemplified by the quote from Armistead Maupin's *Tales of the City*, which opens this chapter.

Anecdotal examples of intersexual mate competition can also be found scattered throughout the ethnographic literature. For example, Devereux (1937) described a situation in which a Mohave man, named Kuwal, recounted a quarrel between his previous partner (an *alyha*, i.e., gender nonbinary/transgender androphilic male) and his new wife. Kuwal stated that the *alyha* "turned up at my house and wanted to fight with my wife…. I was in the house and heard the noise of a fight. My wife and the *alyha* were fighting in the yard outside…. [The *alyha*] picked up a stick and tried to beat my wife with it" (Devereux, 1937, pp. 521–522). Peacock (1968, pp. 203–204) describes another example in which Javanese "women condemn the transvestites [*waria*] because the transvestites seduce their husbands." In reference to the indigenous people of the northwest Amazon, Sorenson (1984) notes that "young men as they return, glistening, from bathing are regarded as especially attractive by members of both sexes" (p. 185). Women attempt to ambush the visiting men if they happen to see them going to bathe alone. Men, in turn, try to seduce the visitors when they go to bathe to keep them away from the local women. Sorenson (1984) notes that this strategy effectively lessens the chances that the visiting men will be seduced by village women. Among the Mpondo (South Africa), intersexual mate competition seemed to underpin tensions in "marriages" between older ("husbands" or *xibondas*) and younger men ("boys" or *tinkonkaka*) working in gold mines

during the first half of the twentieth century (Dunbar Moodie et al., 1989). For example, one Mpondo informant stated that as a "boy," he was not able to get a woman in town because his husband was very jealous.

Many examples of intersexual mate competition may have gone completely unreported to date, simply because researchers lack any sort of theoretical framework for even *recognizing* the existence of such interactions, let alone interpreting them. Here, we move beyond anecdotal accounts of intersexual mate competition between women and same-sex attracted males by documenting the phenomenon more systemically in two different cultures: Samoa and the Istmo Zapotec of Oaxaca, Mexico. In Samoa, transgender androphilic males, known locally as *fa'afafine*, predominate in the population, and cisgender androphilic males are very rare by comparison. Among the Istmo Zapotec, both cisgender and transgender male androphiles are present in the population and occur at appreciable rates. Collectively, they are known locally as *muxes*. Cisgender *muxes* are referred to more specifically as *muxe nguiiu*, whereas transgender *muxes* are referred to as *muxe gunaa*.[2]

Intersexual Mate Competition in Samoa

Semenyna et al. (2020) interviewed 128 Samoan women ($mean_{age}$ = 33.96 years, SD_{age} = 11.7, range 19–70) on the island of Upolu in Samoa, a Polynesian island nation in the South Pacific. Of these women, 115 were in heterosexual relationships (26 dating, 89 married) and the remainder were single. All were exclusively heterosexual (Kinsey 0), save one who was bisexual (Kinsey 3). Samoan women were asked whether they had ever experienced a situation in which they and a *fa'afafine* were simultaneously interested in, and competed for, the romantic/sexual attention of the same man. Participants who answered affirmatively were then asked to provide detailed information about how the interaction unfolded (see Semenyna et al., 2020, for further details pertaining to methodology).

Overall, 43 percent of Samoan women reported that they engaged in intersexual mate competition for a man with a *fa'afafine* rival. Of the data we collected, a total of 51 intersexual mate competition narratives were detailed enough for analysis (four narratives lacked sufficient detail). A minority of these events (n = 10) comprised mate acquisition interactions. The remaining majority comprised mate retention interactions, which involved attempts by a *fa'afafine* to poach women's masculine male partner (boyfriend/husband). Thus, mate-poaching attempts (*sensu* Schmitt & Buss, 2001) occurred frequently enough to

allow for further analyses rendering a number of generalizations possible.

Fa'afafine initiated mate-poaching attempts by using a variety of tactics that could occur separately or in combination. In approximately one quarter of intersexual mate competition interactions (24.4 percent), *fa'afafine* competitors capitalized on opportunity by waiting for opportune moments to approach a man when his girlfriend or wife was absent. Waiting for opportune moments is a common mate-poaching tactic among heterosexual men and women in the United States engaged in intrasexual mate competition (Schmitt & Buss, 2001). *Fa'afafine* attempted to manipulate the woman who was their rival in an appreciable number (39 percent) of intersexual mate competition interactions. For example, *fa'afafine* would signal to the woman, either verbally or physically, that they were in possession of the women's partner (26.8 percent of intersexual mate competition interactions). In addition, they would sometimes direct negative inducements toward their female competitor which involved insults, intimidation, threats, and sometimes even violent behavior (22 percent of intersexual mate competition interactions). Most commonly, however, *fa'afafine* would focus their competitive efforts on manipulating the target man (92.3 percent of intersexual mate competition interactions). For the most part, they accomplished this by directing positive inducements toward target men (87.8 percent of intersexual mate competition interactions). Typically, these positive inducement tactics by *fa'afafine* included appearance enhancement, resource display (e.g., offering alcohol), sexual inducements (e.g., offering sex), and most commonly, flirting. On occasion, *fa'afafine* would also attempt to guard the target man by interposing themselves between the target man and his female partner (12.2 percent of intersexual mate competition interactions).

The female partners of target men would, in turn, respond to *fa'afafine's* mate-poaching attempts by using a variety of tactics that could occur separately or in combination. In an appreciable number of intersexual mate competition interactions (34.1 percent), Samoan women attempted to manipulate their *fa'afafine* rival. For example, women would signal to their *fa'afafine* rival, typically in a verbal manner, that the target man was their partner and thus, belonged to them (24.4 percent of intersexual mate competition interactions). In addition, they would sometimes direct negative inducements toward the *fa'afafine* competitor, which could involve intimidation, threats, and, on occasion, even violent behavior (19.5 percent of intersexual mate competition interactions). Samoan women would also adopt coalitional strategies in which they enlisted the help of others in their village, or in other villages, to spy on their boyfriends/husbands and then report back to them. Most commonly, however, women would focus their competitive efforts on manipulating the

target man (90.2 percent of intersexual mate competition interactions). During approximately one quarter of these interactions, women attempted to manipulate the target man by using positive inducements (24.4 percent of intersexual mate competition interactions). Some of the most common positive inducement tactics women directed toward target men included love and caring (e.g., displays of affection) and appearance enhancement (e.g., wearing nice clothes/jewelry/makeup). During a little more than half of all intersexual mate competition interactions (53.7 percent), women engaged in mate-guarding behavior following a *fa'afafine's* mate-poaching attempts. The mate-guarding tactics that women typically employed included concealment (e.g., insisting the target man stay in the house) and, more often, vigilance (e.g., monitoring the target man's movement and behavior and checking the target man's phone messages). Most often, however, women attempted to manipulate the target man using negative inducements (70.7 percent of intersexual mate competition interactions). Typically, the negative inducements women directed toward target men included commitment manipulation (e.g., demands of total commitment) or emotional manipulation (e.g., attempting to make the target man feel guilty) and, most commonly, punishing the target man if he showed signs of committing infidelity (e.g., becoming angry and threatening to end the relationship). The mate retention tactics Samoan women employed during these intersexual competitive interactions bear a striking resemblance to patterns of mate-guarding described among women in the United States during intrasexual competitive interactions (Buss, 1988; Buss & Shackelford, 1997).

In sum, both *fa'afafine* and women employed a variety of competitive tactics, but both directed the majority of their mate-poaching/mate retention behaviors toward the target man. Mate-poaching attempts by *fa'afafine* were not without potential consequences for women. As one forty-year old Samoan woman from the capital, Apia, stated: "we have to really bring our A-game, … especially when the *fa'afafine* are so feminine, like, they're all pretty and stuff … otherwise … 'bye-bye,' and they walk out with the guy while you're standing there looking stupid." Indeed, following 27 percent of these intersexual mate competition interactions, *fa'afafine* succeeded in seducing women's partners. These were typically short-term liaisons, as a number of women reported reconciling with their partners after seeking promises of commitment and future fidelity.

The following anecdotes provide real-world examples of intersexual mate competition between *fa'afafine* and women and, in doing so, illustrate some of the general patterns outlined above. These examples have been edited slightly for brevity and to remove identifying details. The following anecdote was recounted to the last author (PLV) and a *fa'afafine* research assistant by a

married Samoan woman who was forty-six years old at the time and living near the capital, Apia. This particular intersexual mate competition interaction concludes with the *fa'afafine* competitor successfully poaching the woman's boyfriend.

> It was at a nightclub and I was there with my boyfriend. A *fa'afafine* was there and my boyfriend had slept with the *fa'afafine* before. The *fa'afafine* came and grabbed my boyfriend and I grabbed him back and told the *fa'afafine*: "No!" Then the *fa'afafine* took a chair and smashed it on the table and all the glasses broke. And then the *fa'afafine* said "That's my boyfriend." So, I said, "Ok, you take him." So, I dropped him because I was afraid of the *fa'afafine*. The *fa'afafine* was really angry. The guy wanted to get back together with me, but I said "no" because I was afraid the *fa'afafine* might be violent with me. The *fa'afafine* was glaring at me really angry and swearing "Ufa!" [fuck you] and he[3] was so drunk and I was afraid. I thought the next day the *fa'afafine* might come and apologize but she never did. I found out that the *fa'afafine* and my boyfriend had a plan to get together that night, but my boyfriend went out with me instead. The *fa'afafine* was really pissed and found out where I was with my boyfriend [at a nightclub]. So the *fa'afafine* came there looking for my boyfriend and was really, really angry.

Our second Samoan example outlines a conversation that was recounted to the last author (PLV) and a *fa'afafine* research assistant by a married Samoan woman (W) who was forty-one years old at the time and living in a rural village on the island of Upolu. This particular intersexual mate competition interaction concludes with the woman regaining her boyfriend following a *fa'afafine* competitor's temporarily successful mate poaching attempt.

> PLV: You were saying that there have been times when a *fa'afafine* liked …
> W: My boyfriend, yeah.
> PLV: How did the *fa'afafine* show she liked your boyfriend?
> W: Because you know, he came up to him.
> PLV: And did what?
> W: You know, like started kissing him.
> PLV: And then what did you do?
> W: Oh, I just walk up to [the *fa'afafine*] and say, "sorry, excuse me, [the target man] is mine." At that time, [the target man] was my boyfriend—we were not married—so uhh, the *fa'afafine* just turn around and said, "Oh, he's not your husband yet. He's your boyfriend, so he's *everybody's* boyfriend."
> PLV: And what did you say?
> W: Well I was really mad, and I just told [the *fa'afafine*], "Hello! You know I've got what he wants." And then the *fa'afafine* said he's got what [the target man] wants too, but his is tighter. And I said, "Well okay, I have both, then." [laughs]

PLV: Ahh, so what was your boyfriend doing during all of this?
W: Well, since the *fa'afafine* was well dressed, you know, wearing sexy clothes and, yeah, [the target man] chose [the *fa'afafine*].
PLV: Okay. Your boyfriend chose the *fa'afafine*? So, he left you there?
W: Yeah, he left me.
PLV: You said earlier that women have to watch their husbands and boyfriends around *fa'afafine* because *fa'afafine* have good technique?
W: Oh yes. Yes, yes. Yes. Because you know when my boyfriend came back, and then I asked him, you know, "What the heck? Why did you take off?" And then the first thing that he said to me was: "because you know, [the *fa'afafine*] is more experienced than you are."
PLV: So *fa'afafine* have more experience with sex?
W: Yeah, the *fa'afafine* are more experienced in sex than us ladies. Yeah, that's what [the target man] said to me.
PLV: And so that's what attracted him to the *fa'afafine*?
W: Yeah. He said, they're really good at, you know, doing the blowjobs, and you know … just really good in sex.
PLV: And what did you say in response to that?
W: I said, "Well I'm good too." But all he said is, you know, "not good enough."
PLV: Oh. Wow. So … but he did come back to you?
W: No. I went and fought for him.
PLV: Yeah? You fought for him, and he came back to you?
W: Yeah, he came back.
PLV: And how did you fight for him?
W: Umm. Like I tried to be as well dressed as the *fa'afafine*. And you know, like, wearing sexy clothes and makeup. And I started doing like what they were doing. Like doing the blowjobs. And, yeah, and I ended up giving [the target man] the other hole [laughs].
PLV: So [the target man] came back to you?
W: Yeah. He came back to me and, you know, now I stop him from going out. Yeah, I stop him.
PLV: So you told him, "you can't go out"?
W: Yeah, we just stay home and have a drink at home. And I make sure he's always at my side.
PLV: So you're watching him. Keeping him close.
W: Yeah. Keeping an eye on him.

Intersexual Mate Competition among the Istmo Zapotec

Semenyna et al. (2020) interviewed 100 Istmo Zapotec women ($mean_{age}$ = 32.55, SD_{age} = 10.6, range 18–70) in the Istmo region (Juchitán and Tehuantepec districts) of Oaxaca, Mexico. Of these women, the majority were in heterosexual relationships (eighteen dating, fifty-nine married), and the remainder were single. Most were exclusively heterosexual (Kinsey 0; *n* = 93), but some were mostly heterosexual (Kinsey 1; *n* = 6), and one was bisexual (Kinsey 3). Istmo Zapotec women were asked whether they had ever experienced a situation in which they and a *muxe* were simultaneously interested in, and competed for, the romantic/sexual attention of the same man. Participants who answered in the affirmative were then asked to provide detailed information about how the interaction unfolded (see Semenyna et al., 2020, for further details pertaining to methodology).

Overall, 85 percent of Istmo Zapotec women reported that they engaged in intersexual mate competition for a man with a *muxe* rival, yielding 108 unique intersexual mate competition events that were detailed enough for analysis. Six women recounted only acquisition stories, fifty-two recounted only retention stories (accounting for fifty-three stories due to one woman providing two instances), and twenty-four women told independent stories detailing both acquisition and retention competition (accounting for twenty-four instances of mate acquisition and twenty-five instances of mate retention due to one woman providing two stories). To facilitate comparisons with our Samoan data, we focus here on intersexual mate competition interactions involving mate retention, in which a *muxe* attempted to poach a woman's masculine male partner (boyfriend/husband; *n* = 78).

Muxes initiated mate-poaching attempts by using a variety of tactics that could occur separately or in combination. In approximately one fifth of intersexual mate competition interactions (21.8 percent), *muxe* competitors capitalized on opportunity by waiting for a man's girlfriend or wife to be absent before approaching him. In approximately one third of these interactions, *muxes* attempted to manipulate the female participant (32.1 percent of intersexual mate competition interactions). For example, *muxes* would signal to the woman, typically in a verbal manner, that they were in possession of the women's partner (15.4 percent of intersexual mate competition interactions). In addition, during approximately one quarter of these interactions *muxes* would direct negative inducements toward their female competitor which, for the most part, involved attempts to intimidate the woman through direct confrontations involving anger

and bullying (24.4 percent of intersexual mate competition interactions). Most commonly, however, *muxes* would focus their competitive efforts on manipulating the target man (96.2 percent of intersexual mate competition interactions). For the most part, they accomplished this by directing positive inducements toward target men (94.9 percent of intersexual mate competition interactions). Typically, these positive inducement tactics by *muxes* included appearance enhancement, resource display (e.g., offering alcohol), signaling love and affection, sexual inducements (e.g., offering sex), and, most commonly, flirting. These tactics were similar to those employed by *fa'afafine* in Samoa (see above), and some tactics (e.g., appearance enhancement and sexual inducement) are perceived as effective strategies for women in the United States seeking to poach men from existing heterosexual relationships (Schmitt & Buss, 2001).

The female partners of target men would, in turn, respond to *muxes'* mate poaching attempts by using a variety of tactics that could occur separately or in combination. In an appreciable number of intersexual mate competition interactions (35.9 percent), Istmo Zapotec women attempted to manipulate their *muxe* rivals. For example, women would signal to their *muxe* rival, typically in a verbal manner, that the target man was their partner, and thus belonged to them (24.4 percent of intersexual mate competition interactions). In addition, they would sometimes direct negative inducements toward their *muxe* competitor which could involve threats and, on occasion, even violent behavior, but most involved attempts to intimidate characterized by direct and angry confrontations (17.9 percent of intersexual mate competition interactions). Most commonly, however, women would focus their competitive efforts on manipulating the target man (66.7 percent of intersexual mate competition interactions). During one third of all intersexual mate competition interactions (33.3 percent), women engaged in mate-guarding behavior following a *muxe's* mate-poaching attempts. Istmo Zapotec women typically employed vigilance (e.g., monitoring the target man's movement and behavior and checking the target man's phone messages) as their preferred mate-guarding tactic. Most often, however, women attempted to manipulate the target man using negative inducements (60.3 percent of intersexual mate competition interactions). Typically, the negative inducements women directed toward target men included commitment manipulation (e.g., demands of total commitment) or emotional manipulation (e.g., attempting to make the target man feel guilty) and, most commonly, punishing the target man if he showed signs of committing infidelity (e.g., becoming angry and threatening to end the relationship).

In sum, both *muxes* and women employed a variety of competitive tactics, but

both directed the majority of their mate-poaching/mate-retention behaviors toward the target man. Mate-poaching attempts by *muxes* were not without potential consequences for women. Reflecting on an instance of intersexual mate competition that precipitated a breakup with her boyfriend, one twenty-nine-year old woman from Juchitán said: “With all the pain in my heart, I suffered. I denigrated myself as a woman, and my self-esteem dropped to the floor.” Indeed, following 12 percent of these intersexual mate competition interactions, *muxes* succeeded in seducing women’s partners. We suspect that this estimate is a conservative one given that some Istmo Zapotec women may have been unaware of their partners’ clandestine sexual activities with *muxes*.

The following provide real-world examples of intersexual mate competition between *muxes* and Istmo Zapotec women, illustrating some of the general patterns outlined above. These examples have been edited slightly for brevity and to remove identifying details. The following anecdote was recounted to the second author (FRGJ) and an Istmo Zapotec research assistant by a sixty-eight-year old Istmo Zapotec woman from the district of Juchitán in Oaxaca.

> Yes. There was a *muxe nguiiu* that would hug my husband. There was one time that we went out to drink and the *muxe* wanted to hit me. He[4] told me that he had managed to take my husband to the beach just by giving him three beers. The *muxe* would say vulgar things like “I can squeeze; you can’t do that anymore.” I slapped him a couple of times. My husband wouldn’t flirt with him; maybe because I was present. The *muxe* would tell me that when they were alone, they would do things. I was very jealous. I would ask my husband, “Do you prefer me, or the *muxe*? Go with the *muxe* since he says that his pussy still squeezes and mine doesn’t.” My husband said, “No, you’re crazy!” I thought that my husband had something with the *muxe*, but he told me that nothing happened.
>
> One day, while we were working in an agave field, he started to flirt with my husband. I got mad and hit him with an iron—the kind that we heat up using charcoal embers. I hit the *muxe* on the back and I hit my husband on the head. After I hit the *muxe*, he said, “Oh my belly! Oh, I’m going to abort a son! Your husband’s son!” My granny was nearby, and I said, “Oh granny! I swear to God that I feel like I could kill him!” After that, the *muxe* left the farm where we were working. He said he was afraid I would kill him.

It is interesting to note, in the context of the above example, that fear of being killed by a rival has been reported in Euro-American studies of antihomicide ideation (Buss, 2006).

Our second Istmo Zapotec example was recounted to the second author (FRGJ) and an Istmo Zapotec research assistant by a forty-one-year old Istmo Zapotec woman from the district of Tehuantepec in Oaxaca. This particular intersexual mate competition interaction concludes with the *muxe* competitor successfully poaching the woman’s boyfriend.

> When I was 14-years old, I liked a guy who played soccer. He was very handsome and was older than

me; he was around 18 years old. We started to be a couple, but there was a group of *muxes* who were hair-stylists. The soccer players would go to the salon to get their hair cut. It was like a club; the *muxes* would give them massages. There was one *muxe gunaa* who was very flirtatious with my boyfriend, hugging him in front of me. The *muxes* could be more direct than me.

I think that both the *muxe* and I started dating the guy at the same time. I didn't know what to do because I felt that my boyfriend liked how the *muxe* flirted with him. The thing is that it was a difficult situation because you are competing with someone who is not of your own gender. There was a moment where [the *muxe*] was making a big commotion saying that she liked him more than I did. It was such a big scandal that my family forbade me from seeing the guy.

I didn't leave things as they were, though. I talked to my boyfriend and he said, "[the *muxe*] is just my friend. She's *loca* [crazy]; she likes to play like that with me. But I'm not a *mayate* [a cisgender man who routinely has sex with *muxes*], I like you."

One day, I caught my boyfriend having sex with the *muxe*. He couldn't deny it to me anymore. I heard my boyfriend saying to the *muxe*, "Baby … my queen … come here." When I caught them, the *muxe* said to me, "You don't do it to him like I do it. You will never suck it like I do. You're just a little girl." I said, "But you don't have a vagina." When I learned that my boyfriend had that preference for *muxes*, I didn't want to hear from him again. My brother told me, "Your boyfriend has always been a *mayate*." I didn't understand at the time, but eventually I saw things for what they were and ended the relationship.

Discussion

Research by Semenyna et al. (2020) indicates that, in some cultural contexts, intersexual mate competition for masculine men occurs at appreciable rates between women and androphilic males. In both Samoa and among the Istmo Zapotec, intersexual mate competition followed notably similar patterns. In both cultures, intersexual mate competition involving mate retention was more common than intersexual mate competition involving mate acquisition. These mate retention interactions involved androphilic males (i.e., *fa'afafine* or *muxes*) attempting to poach a woman's masculine male partner, often by capitalizing on opportunities such as the woman's temporary absence. In both cultures, androphilic males were more likely to direct their competitive tactics toward the target man, than toward their female competitor. Overwhelmingly, androphilic males in both cultures attempted to secure target men through positive inducements such as flirting and offers of sex and resources such as alcohol. For their part, women in both cultures typically responded to these mate-poaching attempts by aiming to manipulate the target man, not their opposite-sex competitor. They usually did so by punishing the target man if he showed signs of committing infidelity with the androphilic male competitor. Many of these similarities likely relate to the structural constrains of mate-retention interactions, which channel the possible tactics employed by each type of competitor regardless of cultural context.

There were also some interesting differences between Samoa and the Istmo

Zapotec with respect to intersexual mate competition. For example, compared to Istmo Zapotec *muxes*, Samoan *fa'afafine* were more apt to physically signal that they were in possession of a woman's partner during intersexual mate competition interactions. The Istmo Zapotec are less tolerant of sexual interactions between men and *muxes* (Mirandé, 2017) than Samoans are of sexual interactions between men and *fa'afafine* (Petterson et al., 2020), and this may partly account for differences in androphilic males' public use of overt physical contact as a way of signaling ownership over a man. In addition, *fa'afafine* competitors were more likely to direct insults, threats, and even violence toward female competitors, but such tactics were almost never utilized by Istmo Zapotec *muxes.* Instead, *muxes* were more likely to directly confront their female competitors and taunt that they could successfully poach the target man. What might account for these differences? *Fa'afafine* competitors may have been more willing to use violence, on occasion, against their female rivals, in part, because sex differences in aggression are relatively attenuated in Samoa compared to other cultures (e.g., Munroe et al., 2000; Semenyna & Vasey, 2015). Furthermore, anthropologists have described Samoa as a culture in which aggression is a salient aspect of life (Mageo, 1988), meaning acts of violence by androphilic males against women may be relatively less censured compared to other cultural contexts. Compared to the situation in Samoa, Istmo Zapotec women reported that *muxes* were more likely to use signals of love and affection to poach target men. During our interviews among the Istmo Zapotec, many women expressed incredulity at the idea that their husbands/boyfriends would have sex with a *muxe*. For their part, *muxes* may be taking advantage of women's naïveté in this regard by using tactics that their female competitors (mis)interpret as playful and innocent, when in reality, a more serious sexual undercurrent exists. If so, women's incredulity might have led them to (unknowingly) underreport the full extent of *muxes'* successful mate-poaching attempts. As such, the percentage of successful mate-poaching attempts by *muxes* that are reported here should be viewed as a conservative estimate.

Turning to the female competitors, Samoan women used coalitional strategies during intersexual mate competition far more often than did Istmo Zapotec women. As noted, sexual interactions between men and *muxes* are viewed with relatively more opprobrium in Istmo Zapotec society than in Samoa (cf. Mirandé, 2017; Petterson et al., 2020). This is particularly true for men who have female partners. The use of coalitional tactics during intersexual mate competition necessitates broadcasting to others that one's boyfriend/husband is suspected to have sexual interest in, or have actually engaged in sexual activity with, same-sex partners. It is possible that Istmo Zapotec women experience

relatively more shame in such situations and, as such, avoid eliciting help from others in their community to curtail their male partner's suspected or real infidelity.

Conclusion

Sexual selection has favored individuals who demonstrate flexibility in the means by which they compete for mates. To date, competition for mates has been conceived of as an exclusively intrasexual phenomenon. In certain species, the ability to compete for mates may be a more generalized capacity that extends into the intersexual arena (Vasey et al., 2014a). For example, quantitative research indicates that male and female Japanese macaques (*Macaca fuscata*) compete for female sexual partners (Vasey, 1998). Anecdotal evidence suggest that males and females compete intersexually for sexual partners in at least fourteen additional nonhuman species across eight different avian and mammalian orders (Vasey et al., 2014a).

We do not expect that intersexual mate competition will be common in most species, or even in most human cultures. Indeed, using both university undergraduate and community samples, Semenyna et al. (2020) showed that intersexual mate competition occurs at negligible rates in Canada and was perceived (correctly) by women as largely innocuous. Nonetheless, when individuals of one sex prefer same-sex sexual partners, who themselves behave bisexually, then members of the other sex may be compelled to engage in intersexual mate competition to acquire and maintain reproductive partners. Under such conditions, the reality of mating markets become more complicated as individuals must deal with opposite-sex competitors, as well as same-sex ones.

The manner in which intersexual mate competition is manifested will depend on which sex behaves in a relatively more bisexual manner, and this may vary from one population to the next, or over time. For example, in a variety of non-Western cultures where many masculine men behave bisexually—engaging in sexual interactions with both women and androphilic males (e.g., Fernández-Alemany & Murray, 2002; Petterson et al., 2020; Stief, 2017; Whitam, 1992)—intersexual mate competition for male sexual partners may be more prevalent. In contrast, in many Western cultures, female bisexual behavior and attractions appear to be relatively more common (e.g., Gates, 2011) and given this, intersexual mate competition for female sexual partners may occur more often.

Embracing nontraditional model systems, such as those that involve Samoan *fa'afafine* and Istmo Zapotec *muxes* (or even Japanese macaques), can result in

transformative new ways of thinking about the psychology of sexuality. This, in turn, can help reconfigure our theoretical frameworks and correct biased, incomplete, or even erroneous views regarding mating psychology. Like its intrasexual counterpart, intersexual mate competition has the potential to influence the reproductive competitor's opportunities to engage in conceptive sex. Consequently, our understanding of sexual selection, as well as the developmental and evolutionary processes that underpin mating systems, may be improved by investigating the role that intersexual mate competition plays in the acquisition and maintenance of reproductive partners in certain species.

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Notes

1. *Male* and *female* refer to an individual's biological sex, regardless of whether the individual's identity or gender role presentation is boy/man, girl/woman, or otherwise. Because gender nonbinary males are not recognized as *men* or *women* in their cultures, we refer to them here as males but not men.
2. *Muxes* make up approximately 3–6 percent of the male population in the Istmo Zapotec (Gómez et al., 2018), but the precise proportion of *muxe nguiiu* and *muxe gunaa* is not known.
3. Samoans, and indeed *fa'afafine* themselves, refer to *fa'afafine* using both masculine and feminine pronouns, even within the same narrative (or sentence), as illustrated in this passage. This is neither intended as a slur toward *fa'afafine* by participant women nor taken as insulting by *fa'afafine*. It is our experience that rigid fixation on "correct" pronouns, and insistence on their usage, is largely a Euro-American phenomenon.
4. Much like Samoans, Istmo Zapotec individuals, including *muxes* themselves, employ both masculine and feminine pronouns when referring to *muxes*. This pronoun switching is not intended as a slur. In many instances, however, Istmo Zapotec individuals, including participant women, would tend toward using masculine pronouns to refer to *muxe nguiiu* and feminine pronouns when talking about *muxe gunaa*.

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PART IV

Pair-Bonded Relationship Dynamics

CHAPTER 16

Evolving Connections: Attachment and Human Mating Strategies

Gurit E. Birnbaum

Abstract

Sexual urges and affectional bonding are not always interrelated. And yet, within romantic relationships, intimates typically serve as both attachment figures and sexual partners, such that the attachment and sexual systems may influence each other. In this chapter, I review the reciprocal associations between these two systems. I first introduce a model delineating the functional significance of sex in relationship development and the circumstances under which this function is more prominent. Then, I consider the reverse causal direction, providing an overview of the contribution of attachment processes to the construal of sexual encounters, including the kinds of desires that people wish to satisfy and what they view as desirable in partners. I conclude by suggesting future directions for studying the dual potential of sex for either deepening attachment to a current valued partner or promoting a new relationship when the existing relationship is no longer perceived to be worth retaining.

Key Words: Attachment, Sexuality, Gender Differences, Romantic Relationships, Fantasies, Infidelity, Sexual Desire

Sexual urges and affectional bonding are not always interrelated (Diamond, 2013; Fisher, 1998; Fisher et al., 2002). And yet, within romantic relationships, intimates typically serve as both attachment figures and sexual partners, such that the attachment and sexual systems (i.e., evolved psychological mechanisms that govern the social-cognitive regulation of the attachment and sexual domains; Bowlby, 1982) may influence each other (Birnbaum, 2015b, 2016;

Birnbaum & Reis, 2019). In this chapter, I review the reciprocal associations between these two systems. I first introduce a model delineating the functional significance of sex in relationship development and the circumstances under which this function is more prominent. Then, I consider the reverse causal direction, providing an overview of the contribution of attachment processes to the construal of sexual encounters, including the kinds of desires that people wish to satisfy and what they view as desirable in partners. I conclude by suggesting future directions for studying the dual potential of sex for either deepening attachment to a current valued partner or promoting a new relationship when the existing relationship is no longer perceived to be worth retaining.

The Role Played by Sex in the Promotion of Attachment Bonds

Evolutionary and attachment scholars have long argued that sexual desire helps bring potential romantic partners together initially (Berscheid & Reis, 1998; Birnbaum & Gillath, 2006), thereby increasing the likelihood of reproductive acts (Birnbaum et al., 2014). As such, sexual desire should not necessarily affect attachment processes (i.e., people often engage in sex without feeling bonded to their sexual partners; Diamond, 2003). Still, sexual desire is theorized to play a key role in both attracting potential partners to each other and fostering the development of an attachment between them (Birnbaum, 2014; Hazan & Zeifman, 1994).

To be sure, impregnation is not sufficient for the survival of human offspring. The exceptionally long period during which infants are vulnerable presumably encouraged the development of mechanisms that keep sexual partners bonded to each other so that they could jointly care for their offspring and thereby improve their chances to survive and, eventually, to reproduce (Eastwick, 2009; Fletcher et al., 2015; Symons, 1979). An in-depth look at the set of qualities that distinguish human sexuality from that of other mammals suggests that the sexual system is one such mechanism (Birnbaum & Finkel, 2015; Eastwick & Finkel, 2012; Hazan & Zeifman, 1994). Humans, for example, prefer the “missionary” sexual position (Reinisch & Beasley, 1991), which enables them to maintain face-to-face, belly-to-belly contact with a partner during sexual intercourse. Humans also tend to have sex in private and to sleep together afterward (Ford & Beach, 1951; Reinisch & Beasley, 1991). Such behavioral tendencies may instill a sense of closeness that helps build the emotional connection between sexual partners.

Additional suggestive evidence for the attachment-promoting function of sex

derives from neuroimaging research that shows that experiences of sexual desire and romantic love are characterized by similar patterns of brain region activation (e.g., caudate, insula, putamen; Cacioppo & Cacioppo, 2013; Diamond & Dickenson, 2012). These findings hint at the existence of a pathway that enhances affectional bonding through sexual activation. Supporting this possibility, research has shown that the neuropeptide oxytocin, which facilitates emotional bonding (Acevedo & Aron, 2014; Carter, 2014; Young et al., 2014), is secreted in humans during foreplay, sexual intercourse, and the moments preceding orgasm (e.g., Carter, 1992; Filippi et al., 2003; Murphy et al., 1987). Because humans, unlike most mammals, do not limit their sexual interactions to the days that precede ovulation but have sex throughout the menstrual cycle, they likely experience an extended exposure to oxytocin that further reinforces attachment processes (Young & Wang, 2004).

Instead of relying on indirect evidence for the relationship-promoting role of sex, one can ask people directly about the meaning of sex in their life. In describing their beliefs about sexual interactions, people indeed assert that sex may foster intimacy between partners and cultivate their emotional connection (Birnbaum, 2003; Birnbaum & Gillath, 2006; Birnbaum & Reis, 2006). In describing their reasons for having sex, both men and women frequently mention attachment-based motives, indicating that they use sex to intensify their relationships (Meston & Buss, 2007). These accounts demonstrate that people commonly associate sex with emotional bonding. Nevertheless, they do not provide causal evidence for the proposed pathway from activation of the sexual system to the development of attachment bonds.

Such evidence has initially come from a series of experiments showing that following subliminal exposure to sexual stimuli (vs. neutral stimuli), people exhibit greater accessibility of intimacy-related thoughts (e.g., feeling very close to a partner) as well as report greater willingness to initiate new relationships (e.g., disclosing intimate information to a prospective partner) or to strengthen existing ones (e.g., sacrificing for the relationship; Gillath et al., 2008). These experiments indicate that sexual arousal renders people more inclined to deploy strategies that allow them to become more intimate with a prospective new partner or to sustain an ongoing relationship.

Beyond associating sex with relationship promotion, people also act accordingly, engaging in relationship-promoting behaviors (e.g., expressions of intimacy and affection) and having positive feelings about their relationship (Dewitte et al., 2015) when experiencing intense passion for their partners and satisfying sex (Birnbaum et al., 2006; Debrot et al., 2017; Rubin & Campbell, 2012). Even merely fantasizing about having sex with current partners predicts

actual engagement in behaviors that improve the relationship, such as expressing love for the partners or complimenting them (Birnbaum et al., 2019). Overall, sexual satisfaction helps foster a sense of intimate connection between episodes of sexual interaction by inducing an "afterglow" for as long as forty-eight hours following sexual interaction (Meltzer et al., 2017).

THE RELATIONSHIP DEVELOPMENT MODEL OF SEXUAL DESIRE

The literature reviewed above suggests that sex supports the attachment-bonding process. A recently introduced relationship development model of sexual desire (Birnbaum, 2018; Birnbaum & Reis, 2019) delineates how the functional significance of sexual desire vis-à-vis attachment processes varies in individuals, across contexts, and over time. The model postulates that sexual desire functions as a visceral gauge of partner mate value, with higher (vs. lower) desire for potential or existing partners inducing greater efforts toward deepening connections with valued partners. In support of this idea, research has indicated that behavioral cues that signal mate value, such as behaviors that likely facilitate reproductive success via parental investment (e.g., provision of responsiveness and support; Lin et al., 2002), enhance partners' sexual desirability. For example, in a series of studies that observed partners' displays of responsiveness and sexual desire during discussions of personally meaningful life events, responsive partners were perceived as more valued and accordingly aroused more sexual desire (Birnbaum et al., 2016).

For similar reasons, people tend to experience less sexual desire for partners whose behavior indicates that they are less inclined to invest resources in the relationships. In particular, both men and women are less interested in having sex with a partner whose regard for them is uncertain (Birnbaum et al., 2018). Furthermore, partners' hurtful behavior has been found to undermine sexual desire for these partners. Decreased sexual desire, in turn, predicted increased expressions of desire for alternative mates (Birnbaum et al., 2019a), suggesting that sexual desire ensures that merely valued relationships are maintained, rendering relationships that fail to satisfy emotional needs more susceptible to temptations of other, potentially more suitable mates (Birnbaum, 2018; Buss et al., 2017).

The model further proposes that although sexual desire influences the initiation, development, and maintenance of attachment bonds, sexual desire is especially important to relationship persistence at those stages, and in those circumstances, in which the relationship is highly precarious. Having little information about how a partner feels about the self, such as at the outset of relationships, or experiencing a threat to the current relationship are examples

for such circumstances. In these cases, sex can act as a relationship-promoter as people may strategically use it to achieve intimacy and assuage their attachment insecurities.

Research has supported this theorizing, indicating that sexual desire propels the attachment-bonding process in initial encounters. Exposure to sexual cues (vs. nonsexual stimuli), which activates the sexual system and induces sexual arousal, influences the psychological circumstances that heighten the tendency to approach a prospective partner. Specifically, sexual activation heightens people's romantic interest in prospective partners and encourages them to project their desires onto these partners, rendering them appealing and seemingly romantically interested in them (Birnbaum et al., 2020a). Sexual activation not only biases interpersonal perceptions in a way that may help perceivers satisfy their goal of mate pursuit but also motivates people to actually engage in strategies that foster closeness between previously unacquainted people and thereby help set the stage for deepening emotional connections with them.

People tend, for example, to reveal more personal information as well as to provide more responsiveness and help to a prospective partner following activation of the sexual system (Birnbaum et al., 2017; Birnbaum et al., 2019b). Sexual activation has also been found to motivate people to conform to a potential partner's preferences in order to make a favorable impression (Birnbaum et al., 2020b). Activation of the sexual system apparently encourages human beings to connect, regardless of gender. It does so by inspiring interest in potential partners and motivating men and women to impress these partners and become more intimate with them.

Sexual desire is theorized to determine not only whether the individual seeks to invest efforts in deepening an intimate relationship with a prospective partner but also whether an emotional bond between them is actually formed (Birnbaum, 2018). Corroborating this theorizing, a longitudinal study of newly dating couples has demonstrated the reassuring effect of sex, indicating that relationship insecurities (e.g., worries about separation) waned over time, but only among individuals who experienced high levels of sexual desire for their partners and engaged in frequent sexual activity with them (Mizrahi et al., 2016). Physical consolation in the form of frequent sexual activity thus appears to alleviate relationship insecurities that are inherently typical of the early phases of dating (Eastwick & Finkel, 2008), creating an ambiance conductive to the development of genuine intimacy (see also Rubin & Campbell, 2012).

Sex can satiate attachment needs for reassurance and merger in other anxiety-provoking circumstances, such as when the relationship is under threat. Two series of experiments illustrated this notion. In both series, participants

visualized either a relationship-threatening scenario (e.g., a partner considering breaking up) or a non-relationship-threatening scenario (failure on an exam). Then, participants rated their desire to have sex and the reasons behind it (Birnbaum et al., 2011) or described their sexual fantasies (Birnbaum et al., 2008). Participants were particularly likely to endorse pro-relationship motives (e.g., having sex to nurture the current partner) and to experience sexual fantasies that contained attachment-related themes (e.g., perceiving the self and the objects of fantasies as affectionate and pleasing) following the visualization of relationship threats. These findings indicate that people may use sex to mend a threatened relationship.

The intimacy inherent in sexual contact may satisfy attachment needs for security and love also in real life (Birnbaum, 2014; Davis et al., 2004). A recent longitudinal study has indeed found that even though engaging in postconflict sex can be less enjoyable than engaging in sex that occurred independent of conflict, it buffers against the negative relational implications of conflict (i.e., reduced daily marital satisfaction; Maxwell & Meltzer, 2020). It is therefore unsurprising that frequent and passionate sexual interactions are particularly beneficial for the relationships of those who most need it as a relationship-promoter, such as partners who have destructive personality traits (e.g., relationship insecurities and neuroticism; Birnbaum et al., 2006; Little et al., 2010; Russell & McNulty, 2011) or deficits in nonsexual relational dimensions (e.g., poor communication; Litzinger & Gordon, 2005). For these couples, the reassurance conveyed by sexual desire may mitigate the adverse relational consequences of such negative dispositions.

Attachment Processes and the Functional Significance of Sex in Romantic Relationships

Although the sexual system normatively acts as an attachment-facilitating device that encourages investment in emerging and ongoing relationships (Birnbaum, 2014, 2018; Birnbaum & Finkel, 2015), it does not function in a vacuum. Rather, the functional significance of sex in intimate relationships is likely influenced by mental representations of self and others that developed out of early attachment experiences with primary caregivers and became an inherent part of the attachment system's operation (Birnbaum, 2015a, 2016). The attachment system, which is, indeed, the earliest developing social-behavioral system in humans, evolved to increase infants' survival chances (and future reproductive success) by maintaining proximity to supportive figures (Bowlby, 1982, 1973). Over time, the quality of repeated interactions with these caregivers

shapes the way in which individuals perceive themselves and others as well as what they want out of their close relationships, resulting in relatively stable individual differences in attachment orientation (Fraley & Shaver, 2000).

Interactions with attachment figures who are responsive to one's needs promote smooth functioning of the attachment system and instill a sense of attachment security. This sense of felt security affords confidence that one is lovable and that others are supportive in times of need, thereby fostering the consolidation of interpersonal goals that are intended to sustain nurturing intimate relationships (secure attachment orientation; Mikulincer & Shaver, 2016). Chronic failure to attain the primary goal of felt security, which may result from interacting with attachment figures who are either inconsistently available or consistently unavailable, may lead to the adoption of alternative defensive strategies for dealing with the resulting insecurity: hyperactivation of the attachment system, which typifies anxious attachment orientation, and deactivation of the attachment system, which typifies avoidant attachment orientation. Each of these strategies is driven by distinctive fears and is intended to reach different interpersonal goals that help cope with these fears. Hyperactivation strategy is fed by extreme rejection fears and involves protest responses that aim at motivating the attachment figures to attend to one's needs. Deactivation strategy is fueled by intimacy fears and involves flight responses that aim at keeping emotional distance and self-reliance in close relationships (Main, 1990; Mikulincer & Shaver, 2016).

Attachment strategies guide interpersonal interactions over the entire lifespan by shaping the balance of interdependence and autonomy between intimates (Mikulincer & Shaver, 2016). They are therefore likely to affect the functioning of the later-maturing sexual system (Mikulincer & Shaver, 2019; Shaver et al., 1988). A large body of research has shown that individual differences in the functioning of the attachment system help explain variations in the functions sex serves in close relationships; why people engage in sex, what they seek from their partners, and whether and how they get their needs met (Birnbaum, 2015b, 2016; Birnbaum & Reis, 2019).

THE SEXUAL MANIFESTATIONS OF ATTACHMENT SECURITY

Consistent with the idea that attachment security induces a confident state of mind that promotes relaxed engagement in sexual activities (Birnbaum, 2016; Birnbaum & Reis, 2019), securely attached people (i.e., individuals who score low on both attachment anxiety and avoidance) tend to be less preoccupied with relational concerns (e.g., experiencing uncertainty about being loved) and with sexual performance anxieties (Birnbaum et al., 2014, Birnbaum et al., 2006). As

compared to their less secure counterparts, they have more positive views about sexual aspects of themselves (e.g., perceiving the sexual self as passionate and powerful; Cyranowski & Andersen, 1998); they are more erotophilic and accordingly exhibit more positive affective–evaluative responses to sexual cues (Tracy et al., 2003); and they experience more passionate emotions (and fewer negative emotions) during sexual interactions.

This assertive and stress-free approach to sexuality allows securely attached people to express their sexual preferences without deferring to partners' destructive desires (e.g., engaging in unprotected sex; Feeney et al., 2000; Paulk & Zayac, 2013; Tracy et al., 2003) while still being sensitive to their partners' sexual needs (e.g., Birnbaum et al., 2006). Securely attached individuals are better able than insecure individuals to communicate their sexual needs and understand the needs of their partner (Davis et al., 2006; Starks & Parsons, 2014). This effective sexual communication, in turn, improves their and their partner's sexual and relationship satisfaction (Davis et al., 2006; Sprecher, 2006).

Securely attached people's ease with the closeness imposed by sexual activity (Birnbaum, 2015b, 2016) may motivate them to satisfy their sexual urges within committed intimate relationships (e.g., Brennan & Shaver, 1995; Pau et al., 2000; Stephan & Bachman, 1999). Even as early as during adolescence, they differ from their less secure age-mates in the reasons for having sex and in the circumstances in which they choose to do so (Cooper et al., 2006). Secure individuals tend, for example, to engage in sex to promote intimacy and to strengthen the relationship with their current partner. They also prefer affectionate sexual interactions over emotionless ones (Potard et al., 2017; Tracy et al., 2003) and are thus less likely to approve of casual sex and to engage in it (Feeney et al., 1993; Tracy et al., 2003).

Although seemingly counterintuitive, the same self-assured approach to sexuality that comes with attachment security and promotes pleasurable engagement in exploratory sexual activities within a committed relationship (Birnbaum, 2015b, 2016) may explain why securely attached people are more likely than their less secure counterparts to explore consensually nonmonogamous relationships (Moors et al., 2015; Moors, et al., 2019). The management of multiple relationships that involve attachments to more than one person at the same time may be taxing. Enjoying the benefits that multipartner dynamics can offer may therefore require the ability to build a safe environment with one's primary partner—one that can form the foundation for both exploring relationships with others in times of stability and retreating back to it in times of uncertainty (Conley et al., 2013; Selterman et al., 2019). Regardless of whether

securely attached people choose to explore their sexuality within monogamous or consensually nonmonogamous relationships, they evidently have the state of mind that enables them to experience mutual sexual and relational satisfaction in the long run (Birnbaum, 2015b, 2016; Selterman et al., 2019).

Insecure patterns of attachment, in contrast, are likely to interfere with the functioning of the sexual system, inducing self-defeating thoughts and behaviors (Birnbaum, 2015a, 2016). In all likelihood, functioning in a healthy way may become challenging while constantly feeling insecure about being loved, whether this insecurity is manifested in worries about abandonment (i.e., experiencing attachment anxiety) or in discomfort with emotional closeness (i.e., experiencing attachment avoidance). The nature of this disruption of functioning, however, is expressed differently in anxious and avoidant people's sex life (Birnbaum, 2016; Birnbaum & Reis, 2019).

THE SEXUAL MANIFESTATIONS OF ATTACHMENT ANXIETY

The sexual expressions of attachment anxiety can first be observed in late adolescence (e.g., Cooper et al., 2006). In this period, as sexual and romantic explorations turn into a central developmental task, attachment needs become gradually satisfied through intimates (Collins et al.,, 2009; Tolman & McClelland, 2011). Given that sexual activity is a prominent route for seeking closeness to a partner, it is unsurprising that the erotophilic tendencies of anxiously attached individuals (i.e., people who score high on attachment anxiety) (Bogaert & Sadava, 2002) inspire them to subordinate sex to satisfy their otherwise unsatiated needs for merger. However, because they channel not only their hopeful desires into the sexual route but also their self-destructive insecurities, they often end up realizing their worst fears (Birnbaum, 2015b, 2016).

Anxiously attached adolescents' rejection fears may push them, for example, to compromise their own preferences and to submit to their partner's wishes (Tracy et al., 2003), such that they often find themselves engaging in sexual acts in which they otherwise would not have engaged (e.g., Szielasko et al., 2013). Some of these activities (e.g., unprotected sex and drug use; Feeney et al., 2000; Paulk & Zayac, 2013) may have unwelcome consequences, such as being infected with sexually transmitted disease, becoming unwantedly pregnant (Cooper et al., 2006; Cooper et al., 1998), or being the victim of sexual coercion (see review by Karantzas et al., 2016). The same insecurities that endanger anxiously attached adolescents' well-being may make them dangerous to others, as demonstrated by their tendency to impose sexual contact on their partners as a means to obtaining reassurance or reestablishing connectedness (Brassard et al.,

2007; Szielasko et al., 2013).

Relationship worries keep haunting anxiously attached individuals' bedroom into adulthood, such that they continue to use sex for alleviating their relational anxieties (e.g., Davis et al., 2003, 2004). They are attracted to partners who can provide the sense of reassurance that they yearn for (Birnbaum & Reis, 2012; Holmes & Johnson, 2009; Wei et al., 2005) and frequently have sex for reasons that are intended to achieve positive relationship outcomes (i.e., approach sexual motives, such as expressing love or nurturing the partner; Davis et al., 2004; Impett et al., 2008), even within the context of casual sex relationships (Nunez Segovia et al., 2019). And yet, they also have sex for reasons that are intended to prevent negative relational outcomes (i.e., avoidance sexual motives, such as avoiding partner disapproval or reducing the likelihood of partner abandonment; Cooper et al., 2006; Davis et al., 2004; Impett et al., 2008; Schachner & Shaver, 2004) and have been documented to produce the same adverse consequences they were trying to evade (e.g., feelings of resentment that decrease sexual desire and detract from relationship satisfaction; Impett et al., 2005; Muise et al., 2013).

Anxiously attached people's proclivity to sexualize their attachment needs takes other forms, such as sexting to partners in an attempt to make them respond and gain their reassurance (Weisskirch & Delevi, 2011) as well as seeking warmth, emotional involvement, and attention from partners during sexual intercourse (Birnbaum et al., 2006). These desires are also expressed in frequent sexual fantasizing that revolve around mutual nurturing (Birnbaum, 2007b; Birnbaum et al., 2011) and submission themes that carry the potential to relieve, at least temporarily, their need for ensuring responsiveness from a wiser and stronger caregiver (Birnbaum, 2007b; Birnbaum et al., 2011a).

Ironically, however, anxiously attached people are unlikely to reap the relational benefits of fantasizing (e.g., engaging in relationship-promoting behaviors; Birnbaum et al., 2019a) as they are inclined to perceive their partners as less responsive to their needs (as compared to independent observers; e.g., Campbell et al., 2005; Collins & Feeney, 2004; Segal & Fraley, 2016) and thus are less likely to fantasize about them (Mizrahi et al., 2018). To be sure, when they feel that their primary partner fails to satisfy their emotional needs, they are likely not only to fantasize about alternative partners (Birnbaum, 2007b) but also to secure multiple alternatives in real life, either as a destructive attempt to draw the primary partner closer or as a hedging against being abandoned (Girard et al., 2020).

Overall, anxiously attached people's ambivalent construal of sexuality makes them more prone to experience intruding thoughts during sexual activity

(Birnbaum et al., 2014, Birnbaum et al., 2006). Such relational and sexual worries, together with suppressed communication of sexual needs, hamper their ability to abandon themselves to erotic sensations (Davis et al., 2006; Goldsmith et al., 2016), often resulting in sexual difficulties (e.g., sexual arousal problems, difficulties in reaching orgasms; Birnbaum, 2007a; Birnbaum et al., 2006; Burri et al., 2014; Stefanou & McCabe, 2012). Because anxiously attached individuals tend to use the sexual features of their relationship as a marker for their partner's regard for them (Davis et al., 2004), they are likely to misinterpret such sexual difficulties as a sign of rejection, thereby establishing a vicious cycle of sexual and relational insecurities (Birnbaum, 2007a; Birnbaum et al., 2006). This cycle, however, can be broken, given that gratifying sexual experiences can have a therapeutic effect on anxiously attached people's relationships, as much as frustrating sexual experiences can harm them (Birnbaum et al., 2006; Butzer & Campbell, 2008).

THE SEXUAL MANIFESTATIONS OF ATTACHMENT AVOIDANCE

Unlike anxiously attached people, who rely heavily on the sexual route to satisfy their emotional needs, avoidantly attached people (i.e., individuals who score high on attachment avoidance) use sex to avoid intimacy. In adolescence, their intimacy fears are translated into erotophobic attitudes (Tracy et al., 2003) that lead them to either abstain from having sex altogether or to delay the onset of sexual intercourse, while meanwhile engaging in fewer noncoital sexual behaviors (e.g., making out and fondling) than their less avoidant peers (Boegart & Sadava, 2002; Gentzler & Kerns, 2004; Kalichman et al., 1993; Tracy et al., 2003). When avoidant adolescents do start having sexual intercourse, they do so infrequently and to enhance their prestige rather than to promote their relationships (Tracy et al., 2003). For these reasons, avoidantly attached adolescents tend to be less involved emotionally with their sexual partners (Potard et al., 2017) and get less pleasure from their sexual experiences, often intoxicating themselves prior to engaging in sex (Tracy et al., 2003). And yet, their aversion of intimacy may bring some health benefits, as they are more likely to use condoms than their less avoidantly attached counterparts (Feeney et al., 2000; but see Strachman & Impett, 2009, for failure to find a significant association between attachment avoidance and daily condom use).

The tendency to separate sex from psychological intimacy grows with avoidantly attached individuals into adulthood, making them approach sexual interactions in a variety of distancing ways. Specifically, they find prospective partners who share their desire for independence more sexually appealing than those who pine for intimacy (Birnbaum & Reis, 2012; Holmes & Johnson, 2009)

and are inclined to engage in sex for opportunistic reasons, such as self-worth affirmation or coping with negative emotions (e.g., Cooper et al., 2006; Schachner & Shaver, 2004; Snapp et al., 2014). This motivational makeup, along with low commitment to their primary partner (DeWall et al., 2011), may drive them to approve of casual sex (Brennan & Shaver, 1995; Gentzler & Kerns, 2004; Simpson & Gangestad, 1991; Sutton & Gordon-Simons, 2014; Schachner & Shaver, 2002) and fantasize about extradyadic emotionless sex rather than about intimate interactions with their partners (Birnbaum, 2007b).

Avoidantly attached people do not settle for thoughts. Rather, they act out their fantasies and pursue short-term mating strategies, engaging in hook-ups and extradyadic sex with a variety of mates (Bogaert & Sadava, 2002; Gangestad & Thornhill, 1997; Paul et al., 2000; Stephan & Bachman, 1999). They also tend to respond favorably to attempts to seduce them away from their current partners (i.e., mate poaching), primarily when the poaching is for short-term goals (Schachner & Shaver, 2002). The tendency to seek extradyadic mating opportunities is, unsurprisingly, amplified by their primary partner's desire for intimacy, which pushes the avoidant individual to back further away (Beaulieu-Pelletier et al., 2011). Even under the threat of losing their partner, they are less likely to perform mate retention behaviors, which are designed to reduce the risks of infidelity and breakup (Barbaro et al., 2016; Barbaro et al., 2019).

Consensual nonmonogamous relationships are another form of extradyadic involvement that provides an opportunity to dilute emotional closeness with a primary partner and thus may be appealing for avoidantly attached people. And, indeed, they express desire to engage in such relationships (Moors et al., 2015). Nevertheless, avoidantly attached people are less likely than their secure counterparts to actually do so (Moors et al., 2015; Moors et al., 2019), possibly because they lack the levels of trust and intimacy needed to sustain attachment with multiple concurrent romantic partners over the long haul (Barker, 2005; Moors et al., 2015).

Avoidant people detach themselves from their partners not only by being nonexclusive in intimate relationships but also by often masturbating (Bogaert & Sadava, 2002) rather than having frequent sex with them (Brassard et al., 2007). When avoidant people do engage in sex with their primary partners, they are less likely to show them affection and attend to their needs. Ironically, the resulting aversive feelings of alienation (Birnbaum & Reis, 2006; Birnbaum et al., 2006) impede satisfying their own sexual needs (Birnbaum, 2007a; Birnbaum et al., 2014; Cohen & Belsky, 2008; Gewirtz-Meydan & Finzi-Dottan, 2018). The inability to appease intimacy fears stretches even to avoidant people's protected

realm of sexual imagination, where they experience interpersonal distance and hostility themes, which may assuage their excessive need for self-reliance and control in close relationships but at the same time prevent them from experiencing genuine connection with their partner (Birnbaum, 2007b; Birnbaum et al., 2011a).

On the whole, avoidant people are inclined to dissociate sexual activity from emotional bonding (Birnbaum et al., 2006), rendering what is supposed to be the most intimate interaction devoid of romantic feelings (Birnbaum, 2016; Birnbaum & Reis, 2019). Still, under certain nonthreatening circumstances, they may gain the opportunity of having corrective experiences. Engaging in moderately intimate uncommitted sexual encounters is one example for such circumstances. It is well documented that avoidantly attached individuals experience greater physical pleasure while engaging in uncommitted sexual encounters than while engaging in committed relationships, which may arouse their attachment concerns because of the high levels of intimacy that characterize them (e.g., Gentzler & Kerns, 2004, Nunez Segovia et al., 2019). However, within the context of uncommitted sex, they are more likely to enjoy sex in moderately intimate encounters (e.g., "fuck buddies") than in either highly intimate encounters (e.g., "friends with benefits") or low intimacy encounters (e.g., one-night stands; Nunez Segovia et al., 2019). Apparently, encounters that enable avoidant individuals to develop a superficial friendship allow them to experience affection without having to relinquish the independence they covet.

Within the context of committed relationships, partners' displays of nonverbal affection, such as bodily expressiveness of touching, encourage avoidant people to be as much as engaged in a conversation as securely attached individuals, possibly because this covert (and thus more genuine) signal of a partner's trustworthiness enables them to lower defenses sufficiently to feel being cared for (Schrage et al., 2020). In the same vein, frequent and satisfying sex may benefit the relationships of avoidantly attached individuals, as long as it makes them perceive their partner as more responsive to their needs (Little et al., 2010). In this way, sex may reduce avoidantly attached individuals' negative views of others as uncaring, alleviating the fears that typically impair their relationships.

GENDER DIFFERENCES IN THE SEXUAL EXPRESSIONS OF ATTACHMENT INSECURITIES

Evolutionary (e.g., Buss & Schmitt, 1993; Ellis & Symons, 1990) and cultural socialization processes (DeLamater, 1987; Gagnon & Simon, 1973) lead men and women to perceive and behave differently in their relationships (e.g., men are typically less nurturing than women), such that men tend to report higher attachment avoidance and lower attachment anxiety than women (Del

Giudice, 2011; Simpson et al., 2002). Similar processes lead men and women to construe sexuality somewhat differently (e.g., Birnbaum & Laser-Brandt, 2002). Women tend to adopt an emotional–interpersonal orientation toward sexuality and are therefore likely to associate sex with romantic involvement and to be nurturing during sexual interactions. Men, by comparison, tend to adopt an individualistic–recreational orientation and are thus likely to link sex with physical gratification and to seek sexual variety (Birnbaum & Laser-Brandt, 2002; Carroll et al., 1985; O'Sullivan & Byers, 1992). These different approaches may influence attachment dynamics in the sexual realm.

Research has indeed demonstrated that anxiously attached men and women cope differently with anxieties when it comes to sex (Birnbaum, 2015b, 2016). The traditional gender role of male as sexual initiator (O'Sullivan & Byers, 1992) might make anxiously attached men more prone than anxiously attached women to experience rejection, thus exacerbating their vulnerability. To reduce the likelihood of rejection, anxiously attached men are inclined to invest resources in their ongoing relationship rather than to initiate sex with new partners (Birnbaum, 2015b, 2016). Compared with less anxiously attached men, they start having sexual intercourse at an older age and are less likely to approve of casual sex or to cheat on their partners. As a result, they report having fewer sex partners overall (Allen & Baucom, 2004; Cooper et al., 2006; Gentzler & Kerns 2004). Relationship-threatening conditions, which magnify anxiously attached men's insecurity, intensify their proclivity for pleasing the current partner while dismissing extradyadic desires (Birnbaum et al., 2011b), thereby preventing them from using sex to bolster their self-worth (Cooper et al., 2006).

This pattern migrates into anxiously attached men's fantasy world, as they focus on pleasing their partners even there rather than on using sex to feel better about themselves (Birnbaum, 2007b). Nevertheless, in the real world, abandonment fears may drive them to use coercive sex as a means for regaining proximity to partners (Brassard et al., 2007; Velotti et al., 2022) who are unjustly perceived as unresponsive (Campbell et al., 2005; Segal & Fraley, 2016). Over time, anxiously attached men may view sexual interactions with their partner more as a source of frustration than of joy, gradually losing sexual desire for this partner (Mizrahi et al., 2019). Eventually, they may replace authentic intimacy with pornography in the hope to be gratified, if only partially, without having to risk interpersonal rejection, but end up feeling sexually and relationally dissatisfied (Szymaski & Stewart-Richardson, 2014).

Similar relational worries impel anxiously attached women to adopt the opposite, unrestricted orientation to sex. They begin having sex at a younger age than secure or avoidant women and tend to secure alternatives to current partners

in both the real world (Allen & Baucom, 2004; Bogaert & Sadava, 2002; Gangestad & Thornhill, 1997; Gentzler & Kerns, 2004) and their fantasy life, which is marked by emotionless sex scenes with a variety of sexual partners (Birnbaum, 2007b). Anxiously attached women's relational worries also create difficulties in negotiating sexual encounters that increase the likelihood of engaging in risky sexual behaviors (Cooper et al., 1998; Impett & Peplau, 2002) and being sexually abused (Karantzas et al., 2016).

Gender differences in sexual manifestations of attachment avoidance are less conspicuous than those of attachment anxiety. Both avoidant men and women tend to pursue a short-term mating strategy, deploying tactics designed to avoid entangling commitments (Jonason & Buss, 2012), as well as to become emotionally disengaged from their long-term partners (Birnbaum, 2015a). Still, the avoidant effect is more marked in men's sexuality than in women's, possibly because blindness to partners' wishes is amplified by gender role norms that encourage men to value sexual conquest but attenuated by women's nurturing tendencies (Birnbaum, 2015b, 2016). Avoidant men, for example, are less likely than avoidant women to experience sexual fantasies that include romantic themes (Birnbaum, 2007b) and are more inclined to use sex for relationship-irrelevant reasons (e.g., coping with upset feelings), to engage in extra-pair sex (e.g., Birnbaum et al., 2011a; Cooper et al. 2006; Sprecher, 2013), and to objectify women through pornography consumption and sexual coercion (Davis, 2006; Szymaski & Stewart-Richardson, 2014).

On the whole, although attachment insecurities take their toll on both men and women's sex life, women are susceptible to pay a heavier cost for their insecurity, at least in terms of their sexual functioning (Gewirtz-Meydan & Finzi-Dottan, 2018). Both anxiously and avoidantly attached women are more likely than their secure counterparts to suffer from sexual dysfunctions, such as difficulties with lubrication and reaching orgasm as well as painful intercourse (e.g., Birnbaum, 2007a; Dang et al., 2018; Granot et al., 2018; Stephenson & Meston, 2010; van den Brink et al., 2016), which decrease their overall sexual satisfaction (Birnbaum, 2007a; Gewirtz-Meydan & Finzi-Dottan, 2018). This pattern is hardly surprising given that women's sexual functioning is more likely than that of men to be influenced by the relational context (e.g., Baumeister, 2000; Birnbaum et al., 2013; Diamond, 2003), which, in the case of insecure individuals, is likely to be discordant (Mikulincer & Shaver, 2016) and therefore more harmful for women's sex life than it is for men's.

Concluding Comments and Future Directions

Sexuality and attachment, as reviewed in this chapter, are two key components of adult relational life that influence each other, propelling relationship development and determining its fate (along other processes, such as interdependence, commitment, trust; Berscheid & Regan, 2005; Finkel et al., 2017). Gratifying sexual activity can nurture a secure attachment bond, as much as frustrating sexual experiences can undermine relationship quality and stability. In turn, attachment security may facilitate a gratifying sex life for couples as much as attachment insecurities may impair sexual and interpersonal functioning.

And yet, attachment insecurities evolved because, at least under certain conditions, they confer adaptive advantages, proving useful to promote personal and group well-being (Ein-Dor & Hirschberger, 2016; Ein-Dor et al., 2010) as well as to maximize reproduction potential (e.g., undergoing puberty at an earlier age, engaging in earlier sex, and raising more children; Belsky et al., 2010). As such, they may not always damage relationships, as demonstrated in research showing that attachment anxiety, which normatively characterizes fledgling relationships, may help build the connection between new acquaintances by sparking desire between them (Eastwick & Finkel, 2008). While future work should involve therapeutic interventions that explore whether treatment of sexual difficulties helps couples deepen their attachment bond and inoculate it against the lure of attractive alternatives, additional research is necessary to point to circumstances under which sexual expressions of attachment insecurities might be beneficial for personal and relationship well-being.

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CHAPTER
17

Archaeology of Love: A Review of the Ethnographic Exploration of Love around the World

William Jankowiak and Alex J. Nelson

Abstract

The archaeology of love unearths each culture's tangible behaviors and discourse practices and probes them to explore love's origins, its universality. In this chapter we apply a biocultural lens to the ethnographic and ethnological literature on romantic love to summarize the major findings of anthropological inquiries into love's cross-cultural variability and commonalities. By connecting critical ethnographic insights with attention to their implications for evolutionary theorists, we aim to increase dialogue between scholars studying human mating practices who might otherwise presume their theoretical lenses render the other's observations irrelevant. Specifically, we try to reconcile differences between anthropology's major ethnological studies of love and summarize the ethnographic record of love according to themes that highlight the gaps between cultural ideals and behavioral practice: the entwinement of love and pragmatic interests, the continuum of practices between love and arranged marriages, and love in the absence of sexual monogamy. We also summarize ethnographic accounts of how technology is transforming love across diverse cultural contexts. Throughout the chapter we note the universality of specific themes and adaptive patterns that highlight love as both a psychological essence and cultural experience.

Key Words: love, romantic love, ethnography, cross-cultural research, social theory, companionate marriage Cross-Cultural Studies of Love

The study of romantic love as a social and psychological phenomenon came late to social science inquiry. A primary factor behind its late arrival in anthropology was the prevalent twentieth-century epistemological assumption that the subjective was the mirror image of the social. If psychology is a by-product of a culture's beliefs, then it is better to focus on a culture's cosmology and social organization. Given this epistemological axiom, research ignored or studiously overlooked behaviors that did not fit into the prevailing explanatory schema. They were none too sure of what to do with findings that suggested there may be a universal substream independent of a society's cosmology or social organization. A primary factor for love's neglect was the assumption that love was a "European disease" that more "primitive" or earthy cultures had avoided. In effect, they had sex, but Europe had the more "cultivated" art of love. So pronounced was this assumption that most anthropologists, and everyone else, viewed romantic love as a unique creation of Western Europe that began with the French troubadours and gradually diffused into other cultures. In effect, they believed that romantic love is a European contribution to world culture. Given this assumption, social scientists neglected a serious investigation into whether romantic love could exist in less complex societies. The earliest cross-cultural examinations of love, from anthropology's "armchair era," compared British love ideals to missionary and explorer accounts of those they colonized only to conclude that love was a unique achievement of Europeans which savages, and barbarians fell short of though might one day achieve after proceeding through a unilinear cultural evolution (Finck, 1899). Engels (1884) fell into a similar thought trap, though he was intellectually honest enough to comment upon how Europeans also failed to live up to their love ideals.

An investigation into love, the phenomenon it is and is not, requires the adoption of an "archaeological" approach (Foucault, 1969) in which each culture's tangible behaviors and discourse practices are unearthed and probed to explore love's origins, its manifestations, and its variations within and between cultures. To this end, we sought to uncover and explore how and why a specific society comes to value or deny the formation of strong or weak emotional bonds. In this chapter, we provide a conceptual overview of the relevant cross-cultural findings on love. We explore the ethnographic studies of love and their significance as to what they reveal about love's relationship to sex, marriage, and pragmatic interests. Finally, we note the universality of specific adaptive patterns which serve to highlight love as both a psychological essence and a cultural experience.

Excavating Love's Ethnographic Record: The Ethnology of Love

Love did not become a central subject of ethnographic research until the 1990s, when several groundbreaking ethnographies, ethnological surveys, and theoretical theses jump-started what is now an emergent interdisciplinary area of study (love studies). This push began in anthropology with two ethnological comparative studies of accounts of love documented by ethnographers over previous decades. Jankowiak and Fischer's (1992) ethnological survey of ethnographic accounts in the Standard Cross-Cultural Sample (SCCS) and direct accounts from ethnographers explored the cross-cultural prevalence of "passionate love." They drew their definition of love from Charles Lindholm's (1988) early work defining passionate love as "an intense attraction that involves the idealization of the other, within an erotic context, with the expectation of enduring for some time into the future" (Jankowiak & Fischer, 1992, p. 150). They operationalized the definition as being met by the presence of one or more of the following criteria: love recorded as reason for elopement, love suicide, ethnographer observation that they witness people interacting in a state they considered to be loving, and, most important, a culture's folklore or stories that revealed passionate attachment. This highly inclusive approach found romantic love's presence in 91 percent (151 of 166) of the cultures examined despite those accounts of love present consisting almost exclusively of asides by the ethnographers recording them (Jankowiak & Paladino, 2008). A separate cross-cultural study (Buss, 1989) on mate preference in thirty-seven cultures found "mutual attraction and love" proved to be at or near the top in every culture (Buss, 2019, p. 46). These studies challenged the notion that romantic love originated in Europe and suggested that if romantic love was not a human universal, it is a near human universal (Brown, 1992; Fisher, 1998; Jankowiak, 1995b; Jankowiak & Ramsey, 2000).

In contrast, when Charles Lindholm (1998) applied his definition of love more narrowly to the ethnographic record (specifically the Human Area Relations Files), he found cultures exhibited a romantic love "complex" primarily in circumstances featuring high mobility, weak social networks, and limited opportunities for intimacy in larger groups of kin or peers. In this setting, individuals should "attempt to escape from certain types of social contradictions and structural tensions through the transcendental love of another person" (Lindholm, 1998, p. 258), thereby ensuring romantic love is the stronger and more salient reality. In contrast, romantic love will be absent whenever individuals are embedded in a rich web of intimacies that prevent the formation of an all-exclusive passionate love bond. In this setting, Lindholm contends,

individuals are less likely to need, value, or desire to become involved in a romantic entanglement. From this perspective, romantic love's appearance is closely linked to the social contradictions that arise from living in a particular kind of society. It follows, therefore, that romantic attraction should be unknown, or muted, in relatively stable societies that are organized around intimacies other than the pair-bond.

These two studies relied on the same definition of romantic love but used different criteria to discern it in the ethnographic record. The earlier study assumed that elopements, love suicides, and folklore about love and behavior that had at least the surface appearance of deep pair-bonds approximated western notions of love sufficiently to be presumed to stem from similar sentiments and cognitive experiences. The latter study attempted to match Western romantic love notions more closely to those of other ethnographic and historical periods. Due to the paucity of the ethnographic and historical record concerning love, particularly in the 1990s, it was, and remains, unclear if these discrepancies reflect cultural variation in love's emphasis and institutionalization as Robert Levy (1984) theorizes is the case for other complex emotions, or actual variation in the existence of the complex emotion of love itself. Clearly love is only institutionalized under certain social conditions (de Munck et al., 2016; Lindholm, 1998). However, it remains unclear how heavily we can rely on cultural ideals of love to understand love as it is practiced cross-culturally or even whether our existing definitions of love adequately identify love's defining features cross-culturally.

Victor de Munck and his collaborators, began a program of empirical studies attempting to compare the features of cultural models of love cross-culturally through direct survey measures rather than secondary accounts (de Munck et al., 2009; de Munck et al., 2011). They began comparing conceptions of love in the United States, Russia, and Lithuania with other researchers subsequently adapting and expanding their measures to China (Jankowiak et al., 2015) and South Korea (Nelson & Yon, 2018). They identified five attributes or attitudes that form a universal core of beliefs humans hold about what it means to be "in love." These attributes/attitudes were: "I will do anything for the person I love," "I constantly think about the person I am in love with," "romantic love is the supreme happiness of life," "my love makes my partner a stronger and better person," and "sexual attraction is necessary for love." However, they have only covered a small and in some ways homogeneous (all urban industrialized state societies) cross-cultural sample which allows for overlooking the possibility of greater cognitive, and thus cultural, variation.

Love and Sex: Cultural Variation in Erotic Expressions of Love

Over the past thirty years, the ethnographic record of love has vastly expanded in breadth and depth with dozens, if not hundreds, of texts taking up love as a subject of inquiry. These accounts illustrate the cultural variability of ideals and practices of love while challenging Euro-American ideals of where and how "true" love ought to manifest. The seeming inability of human beings to live up to their cultural ideals of romantic love was once a justification for neglecting the topic as a subject of anthropological inquiry. Social scientists, despite evoking notions of love to describe their own feelings and experiences, followed Freud and others in concluding that if the love of others could not be entirely separated from consideration of sex, status, and wealth, then perhaps love was little more than a discursive end to material and corporeal desires.

A few contemporary world religions (e.g., Christianity and Islam) idealize the disentanglement of love from sex. The celibacy of Catholic priests, the Protestant Victorian promotion of female asexuality, as well as the development of asexual new religious communities (Shakers and Oneidans) exemplify one extreme in the creation of institutional and ideological separation of sex from love (D'Emilio & Freedman, 2012). The French troubadours, who wooed women of the court with adoring songs despite barriers of marriage and social status barring the sexual consummation of their professed longing was long (wrongly) thought to be the origin of romantic love not only in Europe but in the world (Reddy, 2001). However, ideals of chaste love have not been the exclusive invention of state-governed societies. The Pashtuns of Northern Pakistan (Lindholm, 1998), Kohistani tribesmen of the Palas Valley in Northwest Pakistan (Knudson, 2009) and the late Keshurs of the mountain region of Khevsureti in Georgia (Manning, 2015) likewise idealized their romantic love liaisons as chaste. However, unlike the troubadours, the men and women of these societies risked death or exile to pursue their clandestine love liaisons and deeply cherished these exclusively extramarital relationships as sources of intense, though ideally sexually unconsummated, erotic intimacy.

Cultural ideals of chaste love likely serve several social ends. Foremost, separating love from sex is intended to control premarital and extramarital sexuality, particularly that of women, preserving the senior generation (e.g., clan elders and parents) control of the reproductive and erotic capital of the junior generation to be used in exchanges between kin groups (Levi-Strauss, 1969). Additionally, proclaiming such affairs to be chaste would have made them more socially acceptable as subjects for artistic expression in song and poetry (Abu-Lughod, 1986; Manning, 2015). Such sanitizing is evident even in many

contemporary popular culture productions such as Hollywood films of the golden era, Bollywood films, Korean melodramas, and telenovelas. The sexual abstinence featured in these mediums did not reflect practice in the United States, India, South Korea, or Latin America. However, in the case of mass media, the purpose was less an attempt to live up to ideals of asexual love and chastity as to discourage the sexuality of youth who, within this construction of adolescence, may be considered too irresponsible to navigate the potential consequences (pregnancy, disease, consent, legal liability) of sexual behavior. The cross-cultural study of adolescence by Alice Schelegel and Herbert Barry (2000) uncovered the senior generation attempts to control the junior generation's sexuality to avoid the formation of a potentially embarrassing or ill-timed tragic love crush. Their finding is consistent with evolutionary analysis that holds the consequence of unregulated reproduction are too serious not to compel humans to be interested in commenting on and interfering when possible in other people's sex lives (Buss, 2019; Symons, 1979). It is unclear if the clandestine relationships of the Pashtuns, Keshurs, and Kohistani remained as chaste as the ideal prescribed or whether their very liminality and incommensurability with marriage was precisely what produced their erotic and idealistic charge, preventing mundane reality from dispelling their romantic fantasies.

The historic examples of ancient China, Japan, and India illustrate that the spiritualization of pair-bonds did not necessitate a separation of love from sex (Pan, 2012; Reddy, 2001; Ryan, 2006). For much of Imperial China's history, sexual desire and affection readily flowed together as Chinese did not conceptualize the mind as separate from the body and readily recognized the connection between sexual desire and affection (Pan, 2016). Ancient Indians likewise intermingled the sexual and the sacred (Reddy, 2001). Similarly, in Medieval Japan where love "meant holism: it included bodily fusion usually taking the form of sexual consummation" (Ryang, 2006, p. 5). It was not until Japan was forced to become part of a globalizing world economy in the late nineteenth century that they self-consciously began adopting Victorian-esque ideals of sexual purity in their quest to be counted as equals rather than aliens among the colonial superpowers (Ryang, 2006).

Economies of Love: The Inexorability of Pragmatic Interest

Love is idealized in the United States, Europe, and numerous non-Western societies as free of utilitarian or instrumental interests (Eerdewijk, 2006; Engels, 1884; Mody, 2008; Shohet, 2017; Stark, 2017; Stout, 2014; Swidler, 2001;

Zelizer, 2005). This ideal reflects a more central component of romantic love, that love ought not to be reducible to sexual gratification, material benefit, or status considerations. Rather, love is understood to be a good in and of itself (Lindholm, 1998). However, the idealization of love as *exclusively* a good in and of itself leads some to question love's authenticity whenever material factors are associated with a "love bond." The ethnographic record demonstrates that love is rarely divorced from pragmatic interests. Fear of deception may often be well founded, as it is not unusual for some men around the world to "deceive women about the depth of their loving feelings, just to gain short-term sexual access (Haslton et al., 2005, cited in Buss, 2019, p.50). However, the idealization of a completely "free gift" of love appears to be an unachievable, even undesirable overcorrection (Venkatesan et al., 2011).

A love bond can be compatible, however, with pragmatic benefits or even a straightforward commercial exchange. For example, sex workers and their clients may feign love or at least deeper affects than they experience to meet their respective ends in their exchanges with one another. These transactional relationships that begin as commercial or semicommercial exchanges can also result in sincere sentiments of love, and even in marriage (Carrier-Moisan, 2017; Cheng, 2010; Meiu, 2017; Parrenas, 2011; Takeyama, 2016; Williams, 2013). Research on transnational marriage, particularly that organized through marriage tours and so-called mail-order-bride services similarly illustrates that pragmatic or egoistic desires do not preclude the desire for or experience of romantic love, which is often hoped to arise after the marriage when the period of courtship is lacking (Constable, 2003, 2005; Freeman, 2012; Johnson, 2007; Kim, 2018; Yamaura, 2020).

The merging of overt pragmatic interests is evident whether there is or is not a lengthy courtship period. Mutual assistance, emotional care, and spousal intimacy are culturally idealized within a complementary sexual division of labor that is organized around a male's material contribution, while women's contribution is linked to their erotic capital, domestic labor, and reproductive potential. In the United States, these sex-linked attitudes continue to persist and are reinforced through dating rituals despite men and women professing commitment to gender equality (Lamont, 2020). In the United States, as is in most cultures, the gendered way in which sex and material support are entwined is only occasionally questioned as conflicting with constructions of romantic love.

It is a common dilemma: How can a subjective state be expressed without a material referent? When folk ideals of affection entail expectations of material support, individuals must still navigate the prevalent norms of gendered

respectability to maintain their reputation of being a moral subject (Cheng, 2010; Eerdewijk, 2006; Harkonen, 2016, 2018; Mody, 2008; Shohet, 2017; Stout, 2014; Wynn, 2018; Zigon, 2013). The negotiation between material expectation and subjective identification is vividly revealed in Qatari young women's preference to idealize romantic love as a desired state of being that is separate from a man's ability to offer desired gifts and monetary aid (Eerdewijk, 2006). For men who have few resources, material provisioning is a costly signal of one's affection, and its absence possible evidence of insincerity, duplicity, or the inability to be a satisfactory provider (Lewinson, 2006; Stark, 2017; Wynn 2018). For example, the northwest Brazilian folk ideal of "true love" does not eliminate other reasons for entering a marriage. For rural Brazilians, a concern with "interests" or economic well-being is a legitimate rationale for marrying (Rebhun, 1999). Likewise, Jankowiak found that many Chinese women were unwavering in their insistence that love and material realities are not in contradiction. For most, a concern with material realities did not indicate or reflect an absence of love. A twenty-four-year-old Chinese woman highlighted the point, telling him: "I do not see the problem, you can have both. One without the other is incomplete" (Jankowiak & Li, 2017, 2018; see also Diamant, 2000). Concurring with this expectation, a South Korean interlocutor proclaimed of her unsuitable suitor: "I did not want to love him, he was too poor" (Baldacchino, 2008, pp. 111–112). Her comment is strikingly consistent with evolutionary analysis of sex differences in mate preference. Women more than men place a higher priority on a man's social status and ability to provide maternal resources. (Buss, 2019; Symons, 1979). This finding of loves' entwinement with material interest is also consistent with the theory of Bourdieu (1984) that our experiences of attraction may well reflect subconscious recognition of a shared class habitus, allowing us to take material interests into account while denying or otherwise naturalizing their existence as matters of taste or shared values and interests. An analysis of a North American courtship narrative by David Lipset (2015) asserts just that, arguing that's experiences of fated love are really to "love one's fate" (p. 168). These observations highlight the value in examining love as it is practiced as well as its idealized discourses. Doing so reveals how love remains a meaningful institution that is based in reciprocity, if not always equality, while seldom being an unconditional "free gift" (Venkatesan et al., 2011).

Elopements, Love-Come-Arranged Marriages, and Arranged Conjugal Love

For most of human prehistory, cultures around the globe likely allowed

individuals free choice in selecting a mate. However, the shift from foraging to agriculture made the family and larger kinship groups the more essential unit. In this new social organization, the paramount concern was family survival and not personal satisfaction or self-development. Within this domain, the senior generation controlled the sexuality of its junior generation through the institution of the arranged marriage.

Although arranged marriages are popularly assumed to occur with little or no contact between the betrothed before the wedding, ethnographic investigations repeatedly discovered daily life often differed from a society's cultural ideal. For example, in the Muslim Sri Lankan community studied by Victor de Munck (1996), love was a precursor to many arranged marriages despite official prohibitions against "clandestine meetings." Several of their institutions in fact encouraged romantic intimacy and did so specifically between those individuals who would later enter an arranged marriage. These couples, upon discovery of their "secret relationship" or to avoid an arranged marriage to a stranger, would threaten elopement or suicide if their parents did not agree to and "arrange" their marital choice. For example, for Dravidian Muslims in Sri Lanka, the true marital ideal was neither the drama and hardship of elopement nor a dispassionate arranged marriage but a "love-come-arranged marriage" (de Munck 1996; see also Ohara & Reynolds, 1970; Rubinstein, 1995; Schmitt et al., 2004). In love-come-arranged marriage cultures toleration of youths' quasi-secret courtship is an effective adaption that signals sexual interest and the potentiality of forming a loving commitment, which also contributes to a couple's reproductive success (Buss, 2019).

The Sri Lankan love-come-arranged marriage pattern is more widespread than previously acknowledged. Indo-Fijians are also willing to tolerate courtship and children self-selecting spouses when religious, class, and racial boundaries are not crossed (Lateef, 1993). In rural western Turkey, marital choice has become idealized even as public courting remains prohibited (Hart, 2007). Consequently, courtships must either proceed from introductions arranged by parents or through clandestine meetings. In New Delhi, India, arranged marriages remain the hegemonic ideal. Legally, citizens are free to marry whomever they choose, but in practice, the legal system and nongovernment agencies work to enforce parents' perceived rights to select the spouses of their children (Grover, 2018; Mody, 2008; Srinivasan, 2020). Young lovers nonetheless try to use a legal elopement as a bargaining chip to persuade parents into turning their relationships into love-come-arranged marriages to avoid tarnishing the reputations of their kin (Mody, 2008). The Chitralis of northern Pakistan likewise seek aid from intermediaries to convert their elopements into a

love-come-arranged marriage and seek support from a politically powerful local leader to intercede with their parents on their behalf (Marsden, 2007). Among Delhi's scheduled classes, a daughter who fails to secure parental approval for her marriage will lose a valuable tool—the ability to return to her parent's home to shame her affines—in any disagreement or power struggle with her husband or in-laws (Grover, 2018). She is often able to convince her parents to agree to an endogamous match. However, in all the above societies, parental and community resistance is most fierce whenever there is an attempt at an intercaste or interreligious coupling (Grover, 2018, Mody, 2008, Srinivasan, 2020).

The concept and practice of love-come-arranged marriage appears to be a bridge between public courtship and secretive arranged marriage cultures. However, the ethnographic reality is predictably more complicated. A marriage based on personal choice is not always based on romantic love or even based on a belief that one must be in love with one's spouse to marry (Kendall, 1996; Srinivasan 2020). Nor are arranged marriages necessarily devoid of loving sentiment. For example, in the 1980s, Chinese urbanites often courted dispassionately and pragmatically, while hoping to fall passionately in love after, rather than before, agreeing to marry (Jankowiak, 1993, 1995c). New Delhians likewise idealize arranged marital relationships as being characterized by a caring, companionate love. In Cairo, Egypt, Marcia Inhorn (2007) observed couples married by arrangement that had nonetheless formed strong love bonds capable of enduring the stresses and costs of infertility and IVF treatment rather than dissolving their relationships as they were often pressured to do. Among Fundamentalist Mormons practicing "placement marriage," whereby religious leadership assign or marry individuals to each other, many, but not all, marriages also have been observed to cultivate deep love attachments (Jankowiak & Allen, 1995). As described in the next section, companionate marriage, as a cultural ideal, has become the predominant marital expectation along with those for some form of courtship and the cultivation of premarital intimacy. The new global companionate marital ideal has not eliminated arranged marriage, which also can be based on an expectation of care, emotional intimacy, and long-term affection.

Institutionalizing Companionate Marriage and the Individualization of Love

Although Jankowiak and Fischer's (1992) study suggests romantic love to be a cross-culturally universal experience, it is less clear how commonly love is an institutionalized ideal, whether love can still be understood as an institution when it is understood primarily as an antisocial, antistructural disruption to social order. The persistence of clandestine romantic relationships despite their

explicit and severe social censure (Knudson, 2009; Manning, 2015) suggest institutions are produced around romantic love even where the relationships in which they are enacted are deemed deviant and antithetical to moral norms. Shanti Parikh (2015) observed that Ugandan elders of Iganga often ignored their youthful romantic pursuits and refused to acknowledge their existence. In so doing, they avoid potentially legitimizing the love relationships they disapproved of, seeing such love bonds as a threat to a family's pragmatic interests.

Even the United States, Europe, Australia, and other societies that have long held norms of free choice in love and marriage have in recent periods refused to acknowledge, and even punished, love relationships that violated their interests, such as through antimiscegenation laws and denial of the right to marry same-sex couples (Grossi, 2014; Povinelli, 2006). Consequently, queer couples in the United States find they must produce their own courtship scripts, lacking suitable love models to emulate in accordance with their understandings and ideals of gender and sexuality (de Munck 2019; Lamont 2020).

The process of urbanization, along with global trade, has enabled the establishment of more liberal legal codes, which is creating fertile soil for the institutionalization of love-based marriages. The shift in economic resource allocation is altering intergenerational relationships and long-standing gender conventions. The material transformation in subsistence has created space for the individualization of love and with it a preference for a companionate marriage.

Companionate marriage as a cultural ideal is one in which "emotional closeness is understood to be both one of the primary measures of success in marriage and a central practice through which the relationship is constituted and reinforced" and where the spousal relationship is prioritized over those with other kin (Wardlow, 2006, p. 4). In *Modern Loves*, Hirsch and Wardlow (2006) suggest that "companionship is a deliberate goal" of these marriages and that marriage is a "project" aimed at "individual fulfillment and satisfaction" and not simply "social reproduction" (p. 4). From an evolutionary perspective this makes sense: One of the ways to ensure a person will stick with you is to have that person fall in love with you and to demonstrate the sincerity of that love by prioritizing the beloved over other kin. Within this context, love should be regarded as "an evolved solution to the problem of commitment" (Buss, 2019, p. 49; Frank, 1988).

The shift from a family based in agricultural production to a wage labor system, which usually resulted in a movement to the city, reduced individuals' kinship obligations (Collier, 1997; Yan, 2003). Freeing individuals from extended kinship obligations was most immediately manifested in a shift in residence toward living separately from parents. Separate residence, linked with

new occupational choices, encouraged the emergence of a more independent self that could successfully prioritize personal interests that enable the transfer of loyalties and affection to the spouse. Similarly, Carla Freeman (2007) provides a solid analysis of how middle-class Barbadians' understanding of marriage shifted from "duties" to more personal forms of satisfaction. Linda Rehbun (1999) discusses a similar generational change in Northwest Brazil where the expectation of marital satisfaction has shifted from respect to also include a desire for greater emotional exchange. Laura Ahearn (2001) discovered married Majars of Nepal, unlike their parents' generation, used letter writings to objectify their affection, which revealed the value they placed on the formation of close marital ties. Rosi and Zimmer-Tamakoshi (1993), working in Port Morsby (capital city of PNG), illustrate how these transitions to companionate marriages can be fraught with difficulty as young people prefer conjugal equality, while respecting their parents' insistence on upholding precompanionate marital customs that can include offering of a bride price. However, companionate marriage ideals are not exclusively products of capitalist markets, urbanization, and the diffusion of cultural ideologies. They are also observed in contexts yet to be fully infiltrated by these forces such as among the Lahu of Yunnan China (Du, 1995, 2002) and the Igbo of Nigeria (Smith, 2006).

The above studies illustrate the tension youthful lovers confront navigating between "modern" ideals and conventional practices. This is especially so when the idea of modernity is rapidly changing. A study of changing themes about love, self, and obligation in American women's magazines found a 1950s popular expression was: "Love means self-sacrifice and compromise" or putting the family before the self (Canican & Gordon, 1988, p. 172). By the 1960s, 1970s, and 1980s, the folk expression had reverted to: "Love means self-expression and individuality" or putting the self before the family (Canican & Gordon, 1988, p. 172). Anthony Giddens (1992) positively interprets the shift away from a companionate love ideal that values coupledom toward the stronger valuation on the self's ability to find fulfillment in, albeit briefer, "pure relationships" in which the couple's bond continues only as long as it meets each individual's needs. This focus on self-fulfillment may contribute to love's increased fragility, but critical theorists and ethnographers have also argued that the fragility of modern marriages arises from their becoming the principal source of individuals' emotional and sexual fulfillment (Baumann, 2003; Beck & Beck-Gernsheim, 1995; Medeiros, 2018; Tran, 2018).

Love and Marriage without Sexual Monogamy

Although many cultures idealize monogamy, the ethnographic record suggests human beings struggle to practice this ideal. Even in the United States and the UK, where polygamy is criminalized and monogamy and fidelity are essential to a good marriage and an enduring love relationship, sexual infidelity is commonplace (Anderson, 2012). Societies that permit polygamy among at least a minority of its members are not known for their elaborated romantic love complexes. In societies where polygynous marriage is institutionalized, it is not unusual for a husband to have more freedom in choosing additional wives based on a loving sentiment (Lewinson, 2006). Likewise, in societies where first marriages are arranged or highly pragmatic, subsequent relationships are often more freely pursued based on personal attraction (Grover, 2018; Jankowiak, 1993; Parry, 2001). Alternatively, the marriage may be a site principally of social and biological reproduction, while romance is sought primarily in extramarital relationships (Gregor, 1995; Harkonen, 2016, 2018; Hirsch et al., 2009; Ho 2012; Osburg, 2013; Stark, 2017; Uretsky, 2016; Wynn, 2018). However, these examples still suggest that love, but not sexual desire, is a monogamous emotion. One study of American college students suggests that feeling love for two individuals simultaneously, at least in a monogamous society, is a painful and difficult experience, perhaps due to the cognitive dissonance that stems from the contradiction between desire, the need to keep one or more of the lovers secret from the other, or the psychological dissonance that arises from reordering a person's motivational hierarchy that makes it difficult for two people to form a primary love bond. Even where extramarital relationships are widespread, it appears nearly a cultural universal that one must discretely conceal or "keep secret" their affairs from their lovers (see Anderson, 2012; Gregor, 1995; Harkonen, 2016; Hirsch et al., 2009; Ho, 2012; Lepani, 2012; Lewinson, 2006; Medeiros, 2018; Osburg, 2013; Wynn, 2018). To date, no one has offered a satisfactory cultural explanation for this human universal. From an evolutionary perspective, the silence is a sensible response as public awareness can create reputational damage to all in involved, limiting future mating opportunities through the dissolution of the marriage (Betzig, 1989) or increased difficulty finding future mates (Buss, 2019).

The ethnographic cases that most strongly challenge the universality of jealousy and the naturalization of monogamy are those of polyamorous and polyandrous relationships. Polyandrous and polyamorous families contest the notion that love is lessened when it is directed at multiple love objects (Bhattachacharya, 2017; de Munck, 2019; Deri, 2015). However, the efforts couples go through to mitigate jealousy in these relationships suggest there is a deep-seated preference to form exclusive emotional bonds. It further suggests

that jealousy is an evolved adaption that encourages mates to actively "guard" and assess the degree of their partner's commitment. In many contexts, jealousy is not perceived as a negative emotion but rather can be viewed as evidence of a partner's caring and thus, love (Buss, 2000). In polyandrous marriages, the regular absence of one or more of the husbands may mitigate feelings of jealousy and enhance feelings of exclusivity. Similarly, polygamist couples in Mormon fundamentalist communities manage jealousy between cowives by avoiding displays of physical intimacy with one wife in front of another and by denying a preference of having greater affection for a specific wife, a point echoed by a husband who casually remarked he always tells his wives he loves them equally, but (with a wink) admitted he does not (Jankowiak, 2021).

Polyamorists assert that their feelings of jealousy are a consequence of socialization in a monogamous society and not innate to human psychology (de Munck, 2019; Deri, 2015). But jealousy is a recurrent problem among the Mosso, who have no cultural ideology that supports monogamy, institutionalize sexual choice as a near absolute, and where paternity is socially all but inconsequential (Shih, 2010). This suggests that desires for emotional exclusivity in love may not be purely culturally constructed by ideals of monogamy. In effect, humans are more emotionally monogamous than they are sexually monogamous (Jankowiak & Paladino, 2008).

Technology, Cyborg Love, and Globalization

The potential for technology and the dissemination of ideas through mass media and global flows of people is an exciting, essential, and yet understudied domain for understanding shifting practices and ideologies of love. Some of the early technologies of love predate the modern era. Letter writing, novels, and their oral precursors, songs, and poetry, contributed to the development of the early cultural traditions of romance that we have records of, and these technologies and mediums have become even more important as they become accessible to larger portions of the population through improved public education, literacy, and postal systems (Ahearn, 2001; Kwon, 2014; Parikh 2015). Oral and written stories of love are ubiquitous in the ethnographic and literary record (Gottschall & Nordlund, 2006; Lee, 2007; Pan, 2016; Ryang, 2006; Singer, 2009). These stories convey social norms, acting as means of social control, but are also acts of sociality and even social critique and subversion.

From Folktales and Love Magic to Transnational Mass Entertainment Media

The importance humans place on love is made most apparent in its centrality as a muse for artistic expression. Love as a theme is ubiquitous in folktales, songs, and novels. The world's first novel, *The Tale of Genji*, is an easily recognizable depiction of romantic love. Europeans long ascribed the invention of love to the songs of French troubadours and countless cultures utilize singing in their courtship rituals. Australian Aborigine Waipuddanya men sing magical love songs for help in securing a mate (Gioia, 2015, p. 9). The Aborigines of northeast Arnhem Land in northern Australia create a "romantic atmosphere with their sexually charged ritual songs" (Berndt, 1978 p.10). In southwest China, the Lahu sing romantic songs interactively between two lovers in semipublic settings as part of courtship and may form love suicide pacts for through song as well (Du, 1995, 2002). The Lahu illustrate the love song's role in ritualizing courtship in a culturally appropriate and readable manner on the one hand and its use in social subversion in the case of love suicide songs on the other.

TV melodramas, like folktales and songs before them, illustrate the antistructural lure of romantic love while also conveying hegemonic and emergent ideologies. TV romances can be tools of both emancipation and social control. For example, in rural Guatemala, telenovelas have been observed to challenge hegemonic gender roles (Verheijen, 2006). Similarly, telenovelas in Northeast Brazil have likely contributed to women's shifting attitudes toward marital fidelity, transforming men's extramarital sexual pursuits from unwelcome "annoyances" into acts of unacceptable disrespect, clear signs of the absence of romantic love, and grounds for divorce among Afro-Brazilian women (Medeiros, 2018). In South Korea, melodramatic romantic dramas offer romantic inspiration that sometimes challenges familial, class, and sexual norms, and, at other times, serve as cautionary tales of the consequences of such transgressions (Baldacchino, 2014). Syrian romantic teledramas also regularly serve as cautionary tales against premarital sex and lengthy engagements, though others problematize the sexual double standard applied to Syrian women's purity (Joubin, 2020). The themes of these transnational romantic dramas and songs are frequently ascribed to "modernity" for their contrasts with tradition (Baldacchino, 2008; Marsden, 2007). However, ancient portrayals of love are no less recognizable depictions of romantic love than today's Hollywood films, and both mediums create their appeal by simultaneously imagining the romantic possibilities of defying social convention while reaffirming the logics and barriers to doing so.

Love Augmented: Love Letters, Text Messages, and Online Dating

Humans do not only make tools for war, hunting, or agriculture; they create tools for love as well. While numerous material products have romantic significance, jewelry; clothing; flower arrangements, which may symbolize a relationship or express desire; writing; and conveying love letters have special significance. Communicating one's feelings, intentions, and desires through writing serves multiple purposes and has several advantages over singing and verbal communication in the context of courtship, while also posing certain risks in some societies. Letters can enable youths to communicate with the opposite sex when public fraternizing is difficult or poses risks to reputation (Ahearn 2001; Mojola, 2014; Parikh, 2015). Letters provide a space for prospective partners to demonstrate their romantic and symbolic capital through the style and content of their writing; their use of poetic phrasing, alliteration, and metaphor; their borrowing from music and poetry; their handwriting, or use of perfumes or illustrations; and their stationary (Janning, 2018; Parikh, 2015). Letters can also enable lovers to express sentiments that they feel too vulnerable or embarrassed to state aloud or in person (Janning, 2018; Parikh, 2015). Like love poems, the medium of which sets them in a liminal space apart from everyday communicative acts, enabling the expression of otherwise taboo sentiments (Abu-Lughod, 1986), letters are a similarly liminal space in which it is culturally appropriate, even expected, to engage in linguistic flourishes and hyperbolic statements that would feel absurd to utter otherwise. In Nepal, love letters were used largely for courtship directed toward marriage (Ahearn, 2001). In Uganda, love letters may be oriented toward marriage or merely toward youthful romantic exploration (Parikh, 2015). Although youths are increasingly shifting their textual communication with established and would-be lovers to digital formats, physical letter writing remains a meaningful, if increasingly rare, practice (Janning, 2018).

Access to the internet and cellular phones has transformed the world and love in unprecedented ways. The ability to communicate synchronously across long distances has enabled couples to maintain their relationships and cultivate intimacy across continents (Beck & Beck Gernsheim, 2014). These tools also create further opportunities for youths to engage with the opposite sex, arrange rendezvous, explore romance, and cultivate love relationships while avoiding detection by family members and teachers who normally police and disapprove of such interactions (Breteau, 2018; de Leon, 2017; Mojuls, 2014; Parikh, 2015). As the experiences of youths in Muscat, Oman illustrate, the opportunities for romance created through the internet and cell phone technology do not necessarily change the considerations for suitable marriage partners, with class, tribal, and religious endogamy continuing to heavily shape youths' evaluations

of suitable potential partners (Breteau, 2018).

Beyond reinforcing homogamy, advancements in cellular and internet communication have also exacerbated class inequalities, serving as class markers as well as enhancing opportunities to those who can access them (Breteau, 2018; Illouz, 2012; Janning, 2018; Mojuls, 2014; Parikh, 2015). It remains to be seen whether social media and dating applications will enrich experiences of love by helping prospective partners to identify one another, widening the pool or prospective partners, and enhancing their ability to communicate and spend time more efficiently with one another when they are physically separated. Eva Illouz (2019) has argued that such applications as Tinder paired with increased social acceptance of casual sex in Europe and the United States are failing to produce relationships that meet women's desires for emotional intimacy. Illouz (2012) has also argued that such dating technologies also make users more selective, making it more difficult to settle for an adequate partner in their search for "the one." Questions of the impacts of these technologies on love relationships and how culture influences their adoption are undoubtedly among the most dynamic and important directions for future studies of the anthropology of love to investigate in the near future.

Conclusion

The anthropology of love has transformed from a field in which questions of love were noted in passing, in footnotes and asides to increasingly forming the secondary or even central subject of ethnographic investigation. A cottage industry of articles and books have resulted, which we have done our best to survey in this chapter. There are numerous ethnographic edited volumes on the anthropology of love covering love's various ethnographic manifestations (Jankowiak, 1995a), cultural variations in the relationship between love, sex and eroticism (de Munck, 1998; Hirsch et al. 2009; Jankowiak 2008; Padilla et al., 2007), of love and marital ideals (Hirsch & Wardlow, 2006), and even regionally focused collections on Africa (Cole & Thomas, 2009), Japan (Alexy & Cook, 2019), and the Middle East (Fortier et al., 2018). This growing ethnographic record will make future comparative studies more accurate while also providing essential background for the development of such studies, which will need to consider variations in the meanings ascribed to love and related institutions.

Although we are excited at the proliferation of ethnographic data on love, we also hope to see a return to comparative research on love to produce answers to questions of love's universal attributes and how social structural, environmental, and psychological factors contribute to the great variation we see in love's

conceptualization and institutionalization. Furthermore, while it is exciting to explore how technology and globalization are transforming love relationships around the world, we also hope anthropologists conducting fieldwork among those least connected to these developments will not neglect to explore love's cultural construction and behavioral expression in those societies whose disconnection from global cultural flows is rapidly coming to an end. We also want to see increasing interdisciplinary engagement to bring to bear the quantitative tools and theories of psychology into discourse with the more nuanced understandings of culture developed in anthropology and sociology to direct the tools of the social sciences more completely to investigating non-WEIRD (non-Western, educated, industrialized, rich, and democratic) societies that can lend support to those interested in the study of human universals as well as challenge the potential ethnocentrism of the discipline's knowledge platforms.

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CHAPTER
18

Marital and Sexual Satisfaction

Andrea L. Meltzer

Abstract

What factors impact the extent to which people are satisfied with their marriages as well as their sexual relationships with their spouses? To address these questions, this chapter reviews the predominant theoretical frameworks and corresponding empirical evidence for the function of marital satisfaction and sexual satisfaction. It begins by highlighting the function of marital satisfaction and describing the predominant theoretical framework used to predict marital satisfaction: interdependence theory. Following this theoretical overview, the chapter discusses biological and environmental factors that lead to differences in people's marital outcomes and provides suggestions for future research in this area. The chapter then turns to sexual satisfaction, providing an overview of the theoretical rationale for why some people are more versus less satisfied with their sexual relationships with their spouses and discusses numerous factors that influence sexual satisfaction in the context of marriage. The chapter concludes by suggesting several novel advances for furthering our understanding of married couples' sexual satisfaction.

Key Words: marital satisfaction, sexual satisfaction, marriage, sex, interdependence theory

Long-term romantic relationships such as marriage are a central component of human social life. Although there is popular belief that marriage rates are declining, a large majority of Americans view finding a lifelong partner and getting married positively (Thornton & Young-DeMarco, 2001), and most adults in the United States will marry at least once in their lifetime (Cherlin, 2010).

Notably, not only do people's long-term relationships facilitate reproduction, the quality of their relationships plays a crucial role in their overall well-being. Indeed, satisfying long-term relationships help people reach important goals, such as those relevant to career, social life, and health (Fitzsimons et al., 2015), and several meta-analyses demonstrate that they are strong and reliable predictors of better mental and physical health (Holt-Lunstad et al., 2010; Proulx et al., 2007; Robles et al., 2014). Merely being married, for example, reduces mortality risk (House et al., 1988). In fact, the effect of poor relationship quality on mortality is as strong as the effects of better-known risk factors, such as smoking and alcohol use, and even stronger than other important factors, such as sedentariness and obesity (Holt-Lunstad et al., 2010).

Not all long-term romantic relationships such as marriage, however, are ideally suited for successfully rearing offspring or fostering personal growth. There are numerous costs and benefits associated with every partnership, and marriages in which the costs outweigh the benefits may be reproductively maladaptive—that is, they may have negative consequences for offspring. Evolutionary perspectives can be used to argue that, just as positive and negative thoughts and emotions may function to help people attain goals that were important throughout evolutionary history (Nesse & Ellsworth, 2009; Oatley & Jenkins, 1999; Plutchik, 2003), indicators of marital quality—specifically, marital satisfaction—may serve as a barometer that gauges the extent to which people's marriages meet their evolved mating needs (also see Conroy-Beam et al., 2015; Li & Meltzer, 2015; Shackelford & Buss, 1997). Consistent with this perspective, recent evidence suggests that marital satisfaction reflects the extent to which people associate their spouses with positive versus negative affect (McNulty et al., 2013). Accordingly, marriages in which the negatives outweigh the positives (and thus do not meet people's evolved needs) should be characterized by dissatisfaction whereas marriages in which the positives outweigh the negatives (and thus meet people's evolved needs) should be characterized by satisfaction. In light of this functional importance of marital satisfaction and the crucial role that marital satisfaction plays in people's overall mental and physical health, a primary goal of this chapter is to (1) review the predominant theoretical frameworks and corresponding empirical evidence for the key factors that purportedly impact people's marital satisfaction and (2) suggest important avenues for future research in this domain.

Of course, one of the most notable ways in which long-term romantic relationships such as marriage differ from other meaningful close relationships, such as friendships and kinships, is sex (Baumeister & Bratslavsky, 1999). From an evolutionary perspective, the ultimate value of sex in romantic relationships is

obvious: Sex leads to reproduction and gene propagation (Alexander & Noonan, 1979). But recent research also suggests that sex plays an important interpersonal role: sex promotes long-term pair-bonding (Meltzer et al., 2017) because it can, at least in part, offset declines in global marital satisfaction over time (McNulty et al., 2016; Yeh et al., 2006). Indeed, two independent, longitudinal studies of newlywed couples demonstrated that spouses who reported higher (vs. lower) sexual satisfaction at a given assessment reported higher marital satisfaction six months later, controlling for their marital satisfaction at that given assessment (McNulty et al., 2016). In light of the important role that sex plays in long-term romantic relationships, another primary goal of this chapter is to (1) review the dominant theoretical frameworks and corresponding empirical evidence for the key factors that purportedly impact people's sexual satisfaction and (2) suggest important avenues for future research in this domain.

Marital Satisfaction

Given the importance of marital satisfaction to people's overall mental and physical well-being (Holt-Lunstad et al., 2010; Proulx et al., 2007; Robles et al., 2014), it is crucial to develop a strong understanding of the factors that impact it. Evolutionary scholars and relationship scientists alike have introduced numerous theoretical frameworks, many of which are accompanied by abundant empirical support, to understand how people evaluate the quality of their marriages. The next section reviews several of these theories and highlights the factors that purportedly influence the extent to which people are happy with their marriages.

Predictors of Marital Satisfaction

According to interdependence theory (Kelley & Thibaut, 1978), which is perhaps the most influential theoretical framework for understanding marital satisfaction, people consider all their positive and negative experiences in their marriages, referred to as *rewards* and *costs*, and they weigh those rewards against those costs to determine the *outcomes* they gain from their marriages. These outcomes are then compared to people's personal standards of what they need and desire from marriage, referred to as their *comparison level*. Interdependence theory posits that people's marital satisfaction is a function of their marital outcomes relative to their comparison level. People are relatively satisfied with their marriages to the extent that their marital outcomes meet or exceed their personal standards; in contrast, they are relatively dissatisfied with

their marriages to the extent that their marital outcomes fall short of their personal standards (Fletcher et al., 1999, Study 6; Valentine et al., 2020, Study 2). Notably, by accounting for people's personal standards, interdependence theory explains how people can draw different conclusions about marriages that offer similar outcomes: people with high personal standards are more likely to be dissatisfied with a given marital outcome whereas people with low personal standards are more likely to be satisfied with the same outcome.

But what factors impact people's personal standards? The ideal standards model (Fletcher et al., 1999), which draws from both social-cognitive and evolutionary perspectives, provides some direction. According to this model, people desire partners who (1) possess characteristics that can enhance intimacy, develop closeness, and foster trust; (2) are energetic, demonstrate vitality, and are physically attractive; and (3) possess qualities that allow them to obtain respect, resources, and interpersonal success. Likewise, people desire relationships that are characterized by (1) closeness and trust, as well as (2) passion and excitement. Nevertheless, as noted, there is variability in the extent to which people desire such partner and relationship qualities.

Some variability may be explained by differences in the adaptive pressures that people faced in the environment of evolutionary adaptedness. Men and women, for example, faced different adaptive problems and thus differentially value these partner and relationship qualities. According to parental investment theory (Trivers, 1972), males and females of any given sexual species require different minimal investments to successfully reproduce, and those minimal investments directly impact their reproductive strategies—including their partner and relationship standards. Among humans, for example, women are obligated to contribute more time and energy to successfully reproduce a single offspring; at a minimum, they invest forty weeks for gestation followed by several months to years of lactation. Men, in contrast, are obligated to contribute far less time and energy to successfully reproduce a single offspring; at a minimum, they invest mere minutes (or seconds!) for copulation. Although men *can* (and often do) contribute much more time and energy than their required minimal investment, parental investment theory purports that women's (vs. men's) greater *minimum obligatory investment* leads women to be more selective when choosing their reproductive partners (particularly their short-term sexual partners; see Kenrick et al., 1993). Consistent with the idea that differences in the adaptive pressures that people faced in the evolutionary environment of adaptedness shape their personal standards, women (vs. men) more strongly prefer partners who (1) can acquire resources, (2) are willing to share those resources, (3) have social status, and (4) are dominant (see Buss, 1989; Regan,

1998); moreover, women are more satisfied with their marriages to the extent that their spouses possess such traits (French & Meltzer, 2019; Meltzer, 2017; Rogers & DeBoer, 2001). In contrast, men (vs. women) endorse higher standards for partner fecundity and thus are more sensitive to partner characteristics that reflect physical health and fertility (i.e., youth and physical attractiveness; Buss, 1989; Kenrick & Keefe, 1992); moreover, men are more satisfied with their marriages to the extent that their spouses are physically attractive and, perhaps more important, partner physical attractiveness is more strongly associated with men's marital satisfaction than women's marital satisfaction (Meltzer et al., 2011; Meltzer et al., 2014).

Additional variability in the extent to which people desire such partner and relationship qualities may be explained by ecological differences. According to life history theory (Chisholm, 1993), living organisms have finite resources such as time and energy, and they must differentially allocate those limited resources to maximize their reproductive success. Whereas some species allocate these resources in ways that enhance reproductive effort at the expense of somatic and personal growth, resulting in earlier and more frequent reproduction, other species allocate these resources in ways that enhance embodied and social capital, which ultimately benefits later reproductive effort, resulting in delayed sexual maturation and fewer offspring. Of note, according to life history theory, such differential allocation often depends on the harshness and instability of those species' early ecologies. Although life history theory has historically been used to understand interspecies differences, psychologists have used life history theory to predict intraspecies differences—specifically, variability in how humans make similar trade-offs (Brumbach et al., 2009; but see Stearns & Rodrigues, 2020). Indeed, recent work demonstrates that humans' early ecologies shape or calibrate their partner standards in young adulthood such that those reared in unpredictable ecologies report relaxed standards for partner warmth and trustworthiness—traits that are more closely associated with intra- and interpersonal growth, but not for partner attractiveness and status—traits that are likely to directly benefit offspring (French & Meltzer, 2022).

Yet another predictor of variability in people's partner and relationship standards is their own self-perceived mate value. Indeed, people higher in self-perceived mate value endorse higher partner standards (i.e., place greater importance on desirable traits in ideal partners) than do people lower in self-perceived mate value, which is likely due, at least in part, to their perceived ability to attain such high-quality mates (Buss & Shackelford, 2008; Regan, 1998). Interestingly, not only do people with such high mate value endorse higher standards compared to people with relatively lower self-perceived mate

value, their higher standards are relatively less flexible and thus such people are more likely to be dissatisfied with spouses who fail to meet their standards (Campbell et al., 2001).

Moving beyond people's personal standards, each couple member's enduring qualities (e.g., personality traits; Botwin et al., 1997) and the ways in which married couples interact with one another strongly predict how satisfied they are with their marriages (Gottman, 1979; Karney & Bradbury, 1995; Kelley et al., 1983)—in part because their own qualities and interactions influence people's perceived relationship rewards and costs. Indeed, social learning theory posits that people learn about their marriages by observing and interpreting their own and their spouses' behaviors such that positive behaviors lead to relatively higher marital satisfaction and negative behaviors lead to relatively lower marital satisfaction. Given the dyadic nature of such interactions, developing a full understanding of relationship processes thus requires observing the behaviors of both couple members (see McNulty et al., 2021), which can prove to be methodologically challenging.

Finally, factors external to people's marriages, including their social, physical, cultural, and historical surroundings, can impact their satisfaction with their marriages (Hill, 1949; Karney & Bradbury, 1995). For example, stressors such as illness, career changes, or the birth or loss of a child combined with (1) the resources available to the couple and (2) each couple member's perceptions of the stressor impact their relationship outcomes. Couples who are able to successfully cope in the face of such stressors (or in the accumulation of stressors over time) can thrive whereas couples who are unable to do so are more likely to experience drops in marital satisfaction over time or even dissolve their marriages (McCubbin & Patterson, 1982). Another external factor that can negatively impact people's marital outcomes is their perceived relationship alternatives (Kelley & Thibaut, 1978). People who perceive many options outside their current marriages may be more likely to dissolve those marriages at times in which they are less satisfied whereas people who perceive relatively fewer alternatives may be more likely to endure in their marriages even if they are unhappy.

Together, this body of work reveals that marital satisfaction is a complex construct. Numerous intrapersonal, interpersonal, and external factors interact to predict when people are satisfied versus dissatisfied with their marriages. Although myriad work has been conducted thus far, numerous important questions remain unanswered. The next section highlights some potential directions for future research as well as the need for such research to adopt complex methodologies and statistical analyses to properly model the dyadic,

ever-changing nature of long-term romantic relationships.

Suggestions for Future Research

People's partner and relationship standards (i.e., their partner preferences) play a notable role in long-term romantic relationship processes. Not only are such preferences theorized to orient people toward the types of long-term partners with whom they are likely to be most satisfied (Buss & Schmitt, 2019; Li et al., 2013; Valentine et al., 2020), they are also theorized to impact the extent to which people are indeed satisfied in those relationships (French & Meltzer, 2019; Meltzer, 2017; Meltzer et al., 2011, 2014; Rogers & DeBoer, 2001; Valentine et al., 2020). Inherent to such logic, of course, is the idea that people are aware of what they want in a partner. But some research has challenged this idea (see Eastwick & Finkel, 2008; Kurzban & Weeden, 2005), suggesting instead that people's partner preferences do not predict their partner choices or how happy they are with those partners. One possible explanation for such inconsistency in the literature may be that it takes time for people to realize whether their chosen partners meet their ideal preferences. That is, people may be willing to choose and form relationships with partners who fail to meet or exceed their partner preferences, but, over time, they become dissatisfied with those partners and ultimately dissolve their relationships. To test this possibility, however, a study would need to span the full course of the relationship (i.e., from before formation through dissolution); and no study to date has adopted such a complex methodology. Nevertheless, despite such contradictory evidence, recent work summarizing a large volume of studies revealed that partner preferences profoundly impact actual mate choice and a host of relationship-maintenance behaviors (Buss & Schmitt, 2019).

Moreover, the majority of research examining marital satisfaction uses self-report measures to assess how satisfied people are with their marriages. There is reason to believe, however, that such self-reports that allow for deliberation are rather biased in that people favor information and interpretations that allow them to perceive their relationships positively (see Fletcher & Kerr, 2010; Gagne & Lydon, 2004; Murray et al., 1996). For example, people reinterpret the details of their prior experiences (Murray & Holmes, 1994), deemphasize the importance of these experiences (McNulty & Karney, 2001), and change their standards (Neff & Karney, 2002), all in ways that allow them to evaluate their relationships positively. One way to reduce such motivational bias may be to move away from deliberative self-reports of marital satisfaction and instead rely more heavily on people's automatic, or implicitly assessed, partner and relationship evaluations.

Providing support for the validity of such automatic measures, a longitudinal study of newlywed couples revealed that automatic partner attitudes assessed just after marriage predicted changes in marital satisfaction over four years whereas self-reported partner attitudes at baseline did not (McNulty et al., 2013). Future research may thus benefit from more frequently employing such automatic measures of marital satisfaction.

Relationship science may additionally benefit from incorporating more physiological measures to gain a deeper understanding of the mechanisms through which individual differences impact marital quality as well as the extent to which marital quality impacts people's psychological and physical health. For example, it is widely recognized that physiology plays an important role in the association between people's early ecologies and their reproductive choices (e.g., prioritizing reproduction vs. somatic growth), but it remains unknown which physiological processes are implicated. Some promising research has recently considered the role of oxidative stress (Blount et al., 2016), but more work in this area is needed. Likewise, other work has demonstrated that brain regions associated with reward and motivation are associated with experiences of intense love (e.g., Aron et al., 2005; Wang et al., 2020; Zeki & Romaya, 2010; for a review, see Ortigue et al., 2010), but it remains unknown which brain regions are implicated in other important relationship processes. For instance, given the role of perceived threat in the association between attachment insecurity and relationship outcomes, it seems reasonable to expect brain regions associated with fear and threat mediate this association (see Chester et al., 2021; Coan et al., 2006). Future research may benefit from exploring these and other physiological mechanisms.

Finally, numerous theories have emerged in relationship science and evolutionary psychology (as well as other areas of biology and psychology) to explain the complexities inherent to long-term relationship maintenance and satisfaction. Future research would benefit from better integrating these theories to develop a more comprehensive theoretical overview of long-term relationships such as marriage (see Durante et al., 2016). For instance, drawing from both life history theory and attachment theory, recent research has demonstrated that people's early childhood ecologies—specifically, the unpredictability of their ecologies—are associated with their romantic attachment orientations in young adulthood (Barbaro & Shackelford, 2019; French et al., 2020; Szepsenwol & Simpson, 2019), providing a fuller understanding of the factors that influence people's mental models of relationship security. Future research should continue to integrate related yet independent theoretical perspectives.

Sexual Satisfaction

Sex is typically a defining feature of romantic relationships (Baumeister & Bratslavsky, 1999), and the extent to which spouses are satisfied with the sexual aspects of their marriage is strongly predictive of their global marital satisfaction (McNulty et al., 2016). Indeed, in what is arguably the most comprehensive study on the association between sexual and marital satisfaction to date, McNulty et al. (2016) used two independent four-year longitudinal studies of newlywed couples to reveal a bidirectional relationship between newly married spouses' sexual satisfaction and marital satisfaction. Those spouses who reported high (vs. low) sexual satisfaction at any given assessment experienced increases in marital satisfaction across the subsequent six to eight months; likewise, those spouses who reported high (vs. low) marital satisfaction at any given assessment experienced increases in sexual satisfaction across the subsequent six to eight months (also see Fallis et al., 2016; Yeh et al., 2006). It is thus important to develop a strong understanding of the ways in which sexual and marital satisfaction are linked.

Recent empirical work has revealed various mechanisms through which sexual satisfaction positively impacts marital satisfaction. One study (Meltzer et al., 2017), for example, used evolutionary perspectives to demonstrate that lingering sexual satisfaction following sexual activity (i.e., sexual afterglow) is a proximal cognitive mechanism through which sex impacts long-term relationship satisfaction. Specifically, consistent with the idea that there are significant costs associated with having constant or uninterrupted sex in long-term relationships (i.e., it reduces resources needed to accomplish other essential goals), Meltzer and colleagues pooled data from two independent, longitudinal studies of newlywed couples to demonstrate that such sexual afterglow functions to sustain the pair bond between acts of sex. Indeed, following a single occurrence of sex, spouses reported elevated sexual satisfaction that lasted forty-eight, but not seventy-two, hours. Crucially, those spouses who reported a stronger (vs. weaker) forty-eight-hour sexual afterglow also reported relatively higher marital satisfaction four to six months later.

Other research recently demonstrated that enhanced automatic evaluations of the partner may serve as another mechanism through which sex promotes marital satisfaction (Hicks et al., 2016, 2018). Hicks et al. (2016), for example, used two longitudinal studies of newlywed couples to reveal that the number of times couples engage in sex predicts changes in spouses' automatic evaluations of their partners that, as other work (Lee et al., 2010; McNulty et al., 2013) has demonstrated, ultimately impacts marital satisfaction. That is, sex served as a

positive relationship experience, and people developed positive associations between those experiences and their partners. Further, spouses who more frequently orgasm during their sexual encounters with their partners similarly report enhanced automatic partner evaluations (Hicks et al., 2018). Together, these findings support not only interdependence theory (Kelley & Thibaut, 1978) and its idea that rewarding interactions such as sexual intimacy (Lawrance & Byers, 1995) benefit long-term relationship satisfaction, but also Birnbaum's (2018) functional model of sexual desire, which posits that sexual desire functions to indicate romantic compatibility and promote relationship stability (also see Maxwell & McNulty, 2019).

Predictors of Sexual Satisfaction

Given the important role that sex and sexual satisfaction play in long-term relationship functioning, it is important to understand the proximal factors that influence whether people are satisfied versus dissatisfied with their sexual experiences with their partners. Fortunately, a robust body of work aims to identify these factors. As that work reveals, however, sex is a complex and multifaceted phenomenon. Some of the more robust predictors that emerge include (1) sexual frequency (albeit with limitations; see below), (2) sexual motivations, (3) sexual communication that fosters emotional intimacy, and (4) sexual novelty.

It has been well documented that the frequency with which couples engage in sex positively impacts their sexual satisfaction (Cheung et al., 2008; Laumann et al., 1994)—but only to an extent. Couples who report engaging in sex more frequently (McNulty et al., 2016) and couples who report spending more time engaging in sex (Blair & Pukall, 2014) report higher satisfaction with their sex lives; nevertheless, this positive association between sexual frequency and sexual satisfaction does not appear to be linear in nature. Indeed, recent data pooled from more than 30,000 people revealed a quadratic association that ultimately leveled off, such that engaging in relatively infrequent sex (i.e., no sex within the prior month) was associated with lower satisfaction than engaging in more frequent sex (i.e., once per week), but that even *more* frequent sex (i.e., several times per week) was not associated with additional increases in satisfaction (see Muise et al., 2016). In fact, experimental research has shown that couples who are directly instructed to double the frequency with which they engage in sex actually report lower sexual satisfaction over time (Loewenstein et al., 2015), perhaps due to the (1) decreased rewards (and potentially increased costs) associated with engaging in sex beyond people's sexual satiety and (2)

perceived “work” associated with engaging in an assigned amount of sex vs. the spontaneous, passion-driven acts of sex that naturally arise in relationships. Together, these findings suggest it is important to consider more than just the *quantity* of sex and that perhaps the motivations driving sex are more important (Impett et al., 2005).

Indeed, research examining sexual motivations reveals that people engage in sex for a variety of reasons, such as physical pleasure, to enhance closeness, to attain a specific goal, or to boost their self-esteem (see Meston & Buss, 2007), and these reasons can be loosely categorized into two different types of motivations: approach motivations (i.e., motivations aimed at obtaining positive outcomes) and avoidance motivations (i.e., motivations aimed at avoiding unpleasant consequences; Cooper et al., 1998; also see Gable et al., 2000). Using daily diaries to assess people’s motivations for engaging in sex with their partners and their subsequent satisfaction with those sexual experiences, Impett et al. (2005) demonstrated that sex is more satisfying when people are motivated to engage in sex for approach reasons such as pursuing sexual pleasure, pleasing their partners, promoting intimacy, or expressing love; in contrast, sex is relatively less satisfying when people are motivated to engage in sex to avoid unwanted outcomes such as avoiding conflict or preventing their partners from becoming angry or disinterested in the relationship. Interestingly, not only are people’s motivations for engaging in sex associated with their own sexual satisfaction, they also impact their partners’ sexual satisfaction (Muise et al., 2013; Peters et al., 2022), suggesting that even one couple member’s motivations for engaging in sex impact the experience for both couple members.

In addition to motivations, the quality of people’s sexual interactions impacts their sexual satisfaction (Forbes et al., 2017). People who consistently reach orgasm or people (particularly men) whose partners consistently reach orgasm report higher satisfaction with their sex lives (Frederick et al., 2017). So, what factors contribute to “high quality” sex? Social psychological research has drawn from the tenets of self-determination theory to suggest that people are happiest with sexual experiences that (1) allow for autonomous choice, (2) demonstrate personal competency, and (3) foster feelings of love and emotional connection (see Brunell & Webster, 2013). Moreover, couples who do (vs. do not) frequently engage in sexual communication (Frederick et al., 2017) that emphasizes responsivity to one another’s sexual needs and desires (Birnbaum et al., 2016; Fisher et al., 2015; also see Reis & Shaver, 1988) report relatively higher sexual satisfaction.

A final factor that can influence sexual satisfaction is sexual novelty, or sexual self-expansion. On average, sexual desire (most notably, women’s but not

men's sexual desire; McNulty et al., 2019) and sexual satisfaction (McNulty et al., 2016) decline over time in long-term romantic relationships; though there is variability across couples such that some couples' sexual desire and sexual satisfaction remain relatively stable over time (Acevedo & Aron, 2009; Ghodse-Elahi et al., 2020). For those couples who are more likely to experience declines in sexual satisfaction over time, one way to maintain or even elevate their sexual experiences may be to engage in novel, self-expanding activities with one another (Muise et al., 2019). Indeed, couples who naturally engage in more novel and self-expanding activities together or couples who are randomly assigned to engage in such activities report higher sexual desire and higher sexual satisfaction compared to couples who naturally (or experimentally) engage in fewer such novel and self-expanding activities together.

Suggestions for Future Research

Given that long-term couples on average experience declines in sexual desire and sexual satisfaction over time, future research would benefit from exploring additional ways in which couples may buffer themselves against such declines. For example, in addition to engaging in self-expanding activities, research suggests couples may benefit from mindfulness training to reduce body- and performance-based cognitive distractions during sexual activity (particularly for women; Dunkley et al., 2015; also see Meltzer & McNulty, 2010). Future sex research should aim to explore additional ways in which couples can avoid, and perhaps even increase, their sexual desire and sexual satisfaction over time.

As noted, sex in the context of long-term relationships functions to promote reproduction (Alexander & Noonan, 1979) and pair bonding (Meltzer et al., 2017). Much of this work, however, has utilized young people in relatively new committed relationships (e.g., newlywed couples) for whom both propagation and pair-bonding are important. As people mature past their fertile years, however, it is possible that the relative importance of these functions changes such that pair-bonding becomes more important than direct reproduction, which may facilitate the reproductive success of children and grandchildren. Moreover, the rate at which this relative importance changes likely differs across men and women. Given that men remain fertile much longer than women, it is reasonable to conclude that the function of sex for men relative to women is incompatible during middle age. Future research may benefit from examining the implications of such incompatibility. It is possible, for example, that such incompatibility drives middle-aged men in long-term relationships to (unconsciously) feel attraction toward younger extra-pair partners with whom they can produce

offspring whereas their older-aged counterparts may be less likely to experience such attraction. Likewise, it is possible that such incompatibility drives middle-aged women to dissolve their long-term relationships so they are free to seek older alternative partners with whom they can develop a stable pair bond whereas their older-aged counterparts are less likely to dissolve their long-term relationships.

Future research would also benefit from considering the ways in which the ever-evolving environment impacts long-term couples' sexual relationships. Humans' modern-day environment vastly differs from the one in which they evolved. According to the evolutionary mismatch hypothesis (Li et al., 2018), such environmental changes have outpaced the time needed for humans' psychological mechanisms to adapt, and this mismatch has important implications for a wide range of human emotions, cognitions, and behaviors (Buss, 2000; Tooby & Cosmides, 1990). The modern medical advancement of hormonal contraceptives, for example, which approximately 140 million women worldwide use (Mørch et al., 2017), and which function to suppress women's natural production of estrogen and progesterone—hormones implicated in women's sexual desire (Gangestad & Thornhill, 2008; Grøntvedt et al., 2017), negatively impact women's sexual satisfaction (Burrows et al., 2012). Indeed, one study recently demonstrated that, in the context of marriage, changes in women's hormonal contraceptive use over time (relative to their use when they first met their spouses) was associated with decreases in their sexual satisfaction (French & Meltzer, 2020). Future research may benefit from further exploring the ways in which hormonal contraceptives impact both women's and men's sexual relationships.

The modern technological advancement of the internet and online matchmaking likely alters people's perceptions of the available pool of alternative relationship partners (Goetz et al., 2019; Li et al., 2018). Given the important role that such alternatives play in people's sexual and relationship satisfaction (Kelley & Thibaut, 1978; Lawrance & Byers, 1995), it is possible that these technological advances interact with humans' evolved psychological mechanisms to negatively impact their sexual and relationship outcomes. As just one example, people who more frequently use the internet and thus are exposed to numerous images of other people who are likely to be cognitively processed as alternative partners may report lower sexual and relationship satisfaction compared to people who less frequently use the internet. Future research may benefit from examining the ways in which these and other modern-day advances impact long-term relationships.

Future research may also benefit from adopting stronger methods for

assessing the implications of sex and sexual satisfaction for long-term relationship outcomes. Assessing aspects of people's sex lives (i.e., sexual occurrences, sexual desires, sexual dislikes) can be highly personal, and participants may be inclined to report socially desirable responses rather than respond honestly. Likewise, assessing couples' recent sexual frequency or people's satisfaction with recent sexual experiences requires people to rely on their memory, which may be subject to recall bias. It is thus essential that relationship scientists develop strong rapport with their participants while also ensuring confidentiality (and, if possible, anonymity), and they should utilize methods that reduce recall-related errors (e.g., diary methods that allow for daily or ecological momentary assessments).

It is also important that future research obtain (1) representative samples that (2) include diverse types of relationships (e.g., same-sex relationships, consensually nonmonogamous relationships) and (3) span the full life cycle (i.e., adolescence through the senior years; see Diamond, 2013; Wood et al., 2018). Using explicit sexual words and phrases in recruitment materials for sex-related research may inadvertently lead scholars to recruit only those participants who are relatively more sexually open or adventurous and willing to answer personal questions about a private facet of their lives compared to the average person, resulting in less generalizable results. Recruiting diverse but representative samples may help to avoid this pitfall.

Finally, future research would benefit from moving beyond correlational research, when possible, to incorporate experimental methods that allow for causal conclusions. By manipulating people's cognitions, biological processes, and/or environmental inputs, research on sexual satisfaction in the context of long-term relationships will help to rule out important confounds and determine the directional nature of key associations. For example, early work examining the association between sexual frequency and sexual satisfaction concluded that more sex is better; but, as noted, experimental research (Loewenstein et al., 2015) that manipulated the frequency of couples' sex revealed that more frequent sex (at least beyond people's natural motivational desires) leads to lower sexual satisfaction. Of course, the personal nature of people's sexual relationships makes many manipulations in this domain challenging (and sometimes ethically inappropriate); nevertheless, our understanding of the factors that enhance people's sexual experiences and thus their long-term relationships will surely benefit from doing so whenever possible.

Conclusion

Given humans' basic need to connect with others (Baumeister & Leary, 1995), and given the role that such close connections play in reproduction as well as people's overall physical and mental health (Holt-Lunstad et al., 2010; Proulx et al., 2007; Robles et al., 2014), it is crucial that evolutionary psychologists, social psychologists, and relationship scientists work together to develop an even clearer understanding of what makes people satisfied with their marriages as well as their sexual relationships with their spouses. Although work thus far has laid a strong theoretical and empirical foundation, future research will benefit from integrating across theories and perspectives. Indeed, work that continues to merge evolutionary perspectives with traditional relationship-science perspectives seems like a promising avenue for field advancement. Likewise, future research should adopt stronger, more intense methodologies that span the entire relationship cycle, which will help to reveal nuances and important variability across relationship milestones and relationship development. Finally, future research would benefit from moving beyond self-report measures and correlational methods to include automatic measures, physiological measures, and experimental methods.

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CHAPTER
19

Sex Differences in Jealousy: The State of the Theory

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Abstract

The theory of evolved sex differences in jealousy has emerged as one of evolutionary psychology's most prominent lines of research. In this chapter, we begin with a review of the theory itself and its statistical implications. We then discuss many of the prominent challenges to the theory. These challenges include a suggestion that sex differences in the interpretation of the questions often used in "sex difference in jealousy" studies confound the results, psychometric concerns regarding the response scales used to assess the sex difference in jealousy, whether actual experiences with infidelity mirror participants' hypothetical reactions, potential cognitive influences on the sex difference in jealousy, ambiguous results regarding physiological manifestations of the sex difference in jealousy, meta-analyses that reach seemingly different conclusions regarding the existence of the sex difference in jealousy, and moderators (including sexual orientation) that attenuate the sex difference in jealousy. Finally, we evaluate the state of the theory in light of the evidence we review, we consider why researchers from different subfields of psychology appear to have such different interpretations of the evidence for sex differences in jealousy, and we outline recommendations for future research directions.

Key Words: sex differences, jealousy, evolutionary psychology

Sex Differences in Jealousy: What Do We Know

In 1992, Buss et al. published "Sex differences in jealousy: Evolution, physiology, and psychology." Based on earlier work by Symons (1979) and Daly et al. (1982), Buss et al. predicted a sex difference in jealousy based on the differential reproductive challenges faced by ancestral men and women. In particular, Buss et al. theorized that men's unique challenge of paternal uncertainty selected for greater jealousy in response to sexual infidelity, whereas women's unique challenge of ensuring paternal investment selected for greater jealousy in response to emotional infidelity. Across two studies, Buss et al found that a significantly greater proportion of women than men chose the emotional infidelity as causing greater distress. Buss et al. also demonstrated the sex difference using physiological measures: Men showed greater electrodermal activity and pulse rate in response to sexual infidelity imagery compared to emotional infidelity imagery, whereas women showed greater electrodermal activity in response to emotional infidelity imagery compared to sexual infidelity imagery.

The Theory of Evolved Sex Differences in Jealousy

The theory of evolved sex differences in jealousy ultimately stems from Darwin's sexual selection theory (Darwin, 1871). As offered by Buss et al (1992), the sex difference in jealousy stems from the unique reproductive challenges faced by ancestral men and women. With respect to men's unique reproductive challenge, Buss et al. (1992) explain:

> In species with internal female fertilization and gestation … males face an adaptive problem not confronted by females—uncertainty in their paternity of offspring…. Compromises in paternity probability come at substantial reproductive cost to the male—the loss of mating effort expended, including time, energy, risk, nuptial gifts, and mating opportunity costs (p. 251)

Likewise, with respect to women's unique reproductive challenge, Buss et al. (1992) explain:

> Although females do not risk maternal uncertainty, in species with biparental care they do risk the potential loss of time, resources, and commitment from a male if he deserts or channels investment to alternative mates (Buss, 1988; Thornhill & Alcock, 1983; Trivers, 1972). The redirection of a mate's investment to another female and her offspring is reproductively costly for a female, especially in environments where offspring suffer in survival and reproductive currencies without investment from both parents. (p. 251)

From these, Buss et al. (1992) hypothesized a sex difference in jealousy:

> Following Symons (1979) and Daly et al. (1982), our central hypothesis is that the events that activate

> jealousy physiologically and psychologically differ for men and women because of the different adaptive problems they have faced over human evolutionary history in mating contexts. (p. 251)

The theory of evolved sex differences in jealousy is, thus, concerned with the relative intensity of four responses: women's jealousy in response to sexual infidelity, women's jealousy in response to emotional infidelity, men's jealousy in response to sexual infidelity, and men's jealousy in response to emotional infidelity. The question of which of these responses the theory compares has been an ongoing source of controversy (see, e.g., Harris, 2005; Sagarin, 2005).

The description of the theory by Buss et al. (1992) leaves this question open. Their description of the theory states only that "these two kinds of infidelity should be weighted differently by men and women" (p. 251). It is possible that these different weightings imply that men will feel more jealous in response to sexual infidelity than they will in response to emotional infidelity and that women will feel more jealous in response to emotional infidelity than they will in response to sexual infidelity. But it is also possible that these different weightings will take a different form (e.g., that both men and women will feel more jealous in response to sexual infidelity than they will in response to emotional infidelity, but that the difference will be greater for men than for women).

Sexual infidelity and emotional infidelity differ in numerous ways beyond the threats of increased paternal uncertainty and decreased likelihood of paternal investment, respectively (e.g., sexual infidelity might be perceived as more volitional compared to emotional infidelity). These differences might mean that sexual infidelity is, on the whole, more jealousy-provoking than is emotional infidelity (or vice versa).

Buss et al.'s (1992) description of the theory is not completely clear about this. However, it is notable that Buss et al. separately describe the ramifications of men's unique reproductive challenge of paternal uncertainty (and the theorized impact of this challenge on responses to sexual infidelity) and the ramifications of women's unique reproductive challenge of ensuring paternal investment (and the theorized impact of this challenge on responses to emotional infidelity). Thus, the theory of evolved sex differences in jealousy is actually a combination of two theories: (1) the theory that men's unique challenge of paternal uncertainty selected for greater jealousy in response to sexual infidelity, and (2) the theory that women's unique challenge of ensuring paternal investment selected for greater jealousy in response to emotional infidelity.

Our view is that these two aspects of the theory could, in principle, be tested separately. However, such tests would require a control condition assessing

men's and women's general reactivity to either sexually related items or emotionally related items or assessing men's and women's reactions to a jealousy-provoking situation outside the domain of sexual or romantic relationships (e.g., sibling jealousy and jealousy among friends). Such a control condition has seldom been included in sex difference in jealousy studies (but see Baschnagel & Edlund, 2016, and Edlund et al., 2019, for exceptions). A control condition would be needed to eliminate confounding factors that could affect the presence, magnitude, and direction of a sex difference in response to sexual infidelity or in response to emotional infidelity. For example, Feldman Barrett et al. (1998) found that women report more intense emotions than men on global, retrospective measures. If a study simply compared women's and men's responses to emotional infidelity, then the phenomenon identified by Feldman Barrett et al. could produce a sex difference that could be misinterpreted as supporting the evolutionary psychological theory. In such a study, the control condition might take the form of assessing men's and women's reactions to strong emotions beyond jealousy (such as global retrospective reactions to falling in love). This control condition would, presumably, manifest the phenomenon identified by Feldman Barrett et al. (and other analogous phenomena) and would, therefore, allow a more valid test of whether women and men differ in response to emotional infidelity.

Buss et al. (1992) and the studies that followed essentially used responses to sexual infidelity as the control condition for responses to emotional infidelity and responses to emotional infidelity as the control condition for responses to sexual infidelity (i.e., each participant's response to the sexual infidelity provides a control for their response to the emotional infidelity and vice versa). This eliminated confounds such as the phenomenon identified by Feldman Barrett et al. (1998), but at a cost of increasing the ambiguity of interpretation of the results. That is, it is unclear in such studies whether an observed sex difference stems from a sex difference in responses to sexual infidelity, a sex difference in response to emotional infidelity, or both.

Perhaps the clearest comparison specified by the theory is the prediction that men, relative to women, will report greater jealousy in response to sexual infidelity compared to emotional infidelity. Buss et al.'s (1992) specification of the theory identifies these relative differences, and Studies 1 and 3 of Buss et al. test this relative comparison. Buss et al.'s analysis of Study 2 adds some ambiguity, as the most straightforward test of the relative comparison would have been the "participant sex by infidelity" type of interaction. Nevertheless, the predicted results for the analyses performed for Study 2 (that men would respond more strongly to sexual infidelity than to emotional infidelity, and that

women would respond more strongly to emotional infidelity than to sexual infidelity) imply an interaction.

Confounding Sex Differences in the Interpretation of Questions

Over the last twenty-eight years, a number of threats to the theory of evolved sex differences in jealousy have emerged. One class of threats to the theory is based on potential confounding sex differences in the interpretation of the questions used to assess responses to sexual infidelity and emotional infidelity. The first of these focuses on sex differences to the extent to which one type of infidelity implies the other. DeSteno and Salovey (1996) refer to this as the "double-shot hypothesis":

> Simply stated, some individuals believe that emotional and sexual infidelity are not independent events…. For instance, emotional infidelity, for certain individuals, may imply that sexual infidelity has occurred or soon will occur. These perceptions of nonindependence, moreover, may be correlated with sex in some samples, with women more likely than men to expect that emotional infidelity by their partners implies associated sexual infidelity. (p. 368)

DeSteno and Salovey (1996) test the "double-shot hypothesis" in two studies in which the differential infidelity implication (the extent to which one type of infidelity implies the other) is used as a simultaneous predictor along with participant sex to predict which type of infidelity participants find more distressing. Both studies replicate the sex difference in jealousy. However, both studies also find that participant sex is no longer a significant predictor when the differential infidelity implication is included in the logistic regression equation. Instead, the differential infidelity implication is the only significant predictor.

Harris and Christenfeld (1996) replicate the sex difference in jealousy and find evidence for an asymmetry in one type of infidelity implying the other. Specifically, Harris and Christenfeld "found … that men think that sex implies love for their partners more than do women, whereas women think that love implies sex more than do men. Later, Harris and Christenfeld note "that the dominant effect was that women think men can have sex without being in love" (p. 365).

Buss et al. (1999) conducted three studies designed to test the plausibility of DeSteno and Salovey's (1996) double-shot hypothesis as an alternative explanation for sex differences in jealousy. Buss et al. asked participants from the United States, Korea, and Japan to respond to a series of forced-choice infidelity dilemmas, some of which were written to preclude a double-shot explanation. American, Korean, and Japanese participants showed significant

sex differences across all six dilemmas with one exception: Japanese participants did not show a significant sex difference on one exclusive infidelity dilemma. In addition, Buss et al. measured differential infidelity implications in the American and Japanese samples. In both samples, a replication of DeSteno and Salovey's logistic regression methodology found that participant sex, but not differential infidelity implications, was a significant unique predictor. Buss et al. conclude that the weight of the evidence supports the evolutionary explanation rather than the double-shot hypothesis. Additionally, Brase et al. (2014) also tested the double-shot hypothesis, with results that replicate those of Buss et al. (1999).

More recently, Kato (2014) posited that the sex difference in jealousy stems from men's greater tendency than women to vividly imagine sexual infidelity. Kato had men and women respond to Buss et al.'s (1992) first forced-choice infidelity dilemma. Consistent with Kato's hypothesis regarding men's tendency to vividly imagine sexual infidelity, the vividness manipulation significantly increased women's (but not men's) tendency to choose the sexual infidelity as causing greater distress.

Response Methodology

The first years of research into the sex difference in jealousy focused primarily on the form of assessment initially used by Buss et al. (1992)—the forced-choice methodology (e.g., Buss et al. 1999; DeSteno & Salovey, 1996; Harris & Christenfeld, 1996). The robustness of this approach was seen in the first meta-analysis of the sex difference in jealousy (Harris, 2003). In this meta-analysis, Harris found that the sex difference in jealousy emerged consistently when assessed via the forced-choice methodology.

Although the sex difference in jealousy using forced-choice measures was beginning to be well established, a number of researchers criticized the reliance on this methodology. The first such critique was made by DeSteno and Salovey (1996) in their "double-shot" paper:

> Although the sex difference in infidelity choice reported by Buss et al. (1992) is readily replicable using the forced-choice paradigm, we have been unable to replicate it using continuous measures asking individuals to rate the amount of distress experienced in response to each type of infidelity.

Subsequently, DeSteno et al. (2002) offered an expanded test of the sex difference in jealousy using continuous measures. DeSteno et al. replicated the sex difference using a forced-choice measure but failed to replicate the sex difference on any of three continuous measures (a scale indicating the intensity

of six emotions experienced in response to sexual infidelity and in response to emotional infidelity, a five-item agree-disagree scale completed in response to each type of infidelity, and a checklist of adjectives completed in response to each type of infidelity). Harris (2003) reviewed these and other studies, finding that the sex difference in jealousy is rarely found in continuous measures. Sagarin (2005) saw the evidence as somewhat stronger but still recognized that the sex difference was more readily replicable using forced-choice measures.

This critique represented a serious challenge to the theory of evolved sex differences in jealousy. If the effect was limited to occurring only when the forced-choice methodology was employed, the effect might reasonably be considered simply an artifact of measurement. However, psychometric decisions made in some of the studies that tested sex differences in jealousy using continuous measures might have limited their ability to find an effect.

The importance of designing scales that maximize useful variance is a key point discussed by Krosnick (1999). Krosnick (1999) offers a number of psychometric recommendations for designing scales such as recommending that unipolar constructs (e.g., “not at all happy” to “very happy”) be measured using 5-point scales, whereas bipolar constructs (e.g., “very unhappy” to “very happy”) be measured using 7-point scales. Regardless of whether the scale is unipolar or bipolar, Krosnick recommends that all points are labeled to ensure that participants interpret the questions similarly (the importance of this point was also demonstrated in Engelbrecht & Edlund, 2016). To more clearly disambiguate whether the scale response format matters, Edlund and Sagarin (2009) directly tested the impact of scaling decisions on the ability to find the sex difference in jealousy. Of the three factors tested, only the labeling of the points significantly moderated the effect, such that scales with all points labeled were less likely to find an effect compared to scales with ends only labeled or midpoint and ends labeled (a finding that runs contrary to the recommendations of Krosnick, 1999; we will return to this issue in a moment).

Two studies using continuous response scales obtained nationally representative samples through TESS (Time-sharing Experiments for the Social Sciences; www.tessexperiments.org). Green and Sabini (2006) reported no difference between men’s and women’s jealousy in response to emotional infidelity and sexual infidelity. However, a reanalysis of the data conducted as part of Sagarin et al.’s (2012) meta-analysis suggested that a significant interaction was present in the theory-supportive direction (when the interaction was analyzed within subjects). Zengel et al. (2013) also collected data through TESS. Zengel et al. found a significant effect for the forced-choice measure but did not find a significant effect for the continuous measure.

Despite these inconsistent findings when sex differences in jealousy are tested using continuous measures, Sagarin et al.'s (2012) meta-analysis found a significant overall effect across studies. Nevertheless, it is clear that the forced-choice measure is a more robust method for finding the effect—a phenomenon that seems at odds with standard psychometric recommendations that dichotomous DVs should be avoided, that continuous measures are preferred, that these continuous measures should consist of 5-point scales when assessing unipolar constructs (e.g., "not at all jealous" to "extremely jealous"), and that all points on the scale should be labeled. However, these recommendations are predicated on an assumption that participants' responses will be distributed across the full range of response options.

In the case of jealousy about a partner's infidelity, it seems likely that this assumption will often be violated because most participants will have extreme reactions to a partner's infidelity. This is evidenced by the number of participants who select the maximum point in many studies using continuous measures (e.g., Green & Sabini, 2006; where approximately three quarters of participants selected the maximum response for emotional infidelity). We suspect that this is the reason that the forced-choice measure is more reliable in finding the sex difference—it prevents participants from indicating that they are equally upset by the sexual infidelity and the emotional infidelity. Instead, participants must choose which type of infidelity is worse, and this forced-choice more readily uncovers the sex difference.

Do Actual Experiences Mirror Imagined Reactions?

In Buss et al.'s (1992) seminal study, participants were asked to imagine their reactions to a number of hypothetical infidelity scenarios while thinking of a relationship that they were currently in, previously had been in, or would like to be in. However, we know that people's ability to accurately imagine their reactions to hypothetical situations can be limited. For instance, studies have shown that people are inaccurate in predicting the intensity and longevity of their affective reactions to a number of situations (e.g., Gaunt et al., 2005), although people rarely make errors in predicting the type of feeling they would experience, such as thinking they would be happy if their favorite team lost.

Some researchers have questioned how these inaccuracies would apply in the context of people's reactions to infidelity. The first study to explore this issue was Harris (2002). Harris first assessed participants' reactions to the traditional forced-choice question, where she found a significant difference in men's and women's responses to the hypothetical infidelity scenarios. Next, she asked

participants if they had ever been cheated on. Participants who said yes were then asked to report how much they focused on each aspect of the infidelity on a 5-point scale ranging from “not at all” to “completely”. Men and women who had experienced an infidelity did not differ significantly in how much they focused on either the sexual or emotional aspects of the infidelity.

Berman and Frazier (2005) also examined men’s and women’s responses to actual infidelity experiences. Berman and Frazier critiqued Harris’s (2002) use of the term “focus” instead of “distress” or “upset” and Harris’s assessment of focus using continuous measures instead of a forced-choice measure, questioning whether the change in term and methodology might have led to the lack of a significant effect. Berman and Frazier presented a single forced-choice question to participants who had experienced an infidelity.

Berman and Frazier (2005) replicated the traditional sex difference among men and women who had not been victims of infidelity (and were, thus, reporting their reactions to a hypothetical infidelity scenario). But Berman and Frazier also found that men and women who had experienced an infidelity showed almost no difference in which aspect of the infidelity was more distressing or upsetting (although, it is worth noting that the small sample size, sixty-four, and the low number of men who had experienced an infidelity, eighteen, makes a confident assertion of the null effect difficult). Harris’s and Berman and Frazier’s failure to find a sex difference in response to actual infidelity experiences dealt a blow to the theory of evolved sex differences in jealousy.

In response to these concerns, Edlund et al. (2006) tested whether sex differences in jealousy would emerge in response to actual experiences with infidelity using both forced-choice and continuous measures that assessed both jealousy and focus. Across two studies, Edlund et al. found significant sex differences in jealousy in participants who had experienced an infidelity using both continuous and forced-choice measures. When asked about focus, the results were weaker although still in the same direction. Finally, Zengel et al. (2013) employed a national panel data collection approach to examine the sex difference in jealousy in a nationally representative sample of Americans. In this sample, the sex difference in jealousy emerged when looking at people’s actual experiences with infidelity on the forced-choice measure but not on the continuous measures.

However, although studies measuring participants’ responses to actual infidelity experiences avoid many problems associated with hypothetical infidelity scenarios, the retrospective nature of these studies raises concerns regarding memory effects. One novel attempt to resolve this employed coding of

in vivo jealousy responses featured on a reality television show (Kuhle, 2011). Kuhle coded a number of episodes of the reality show "Cheaters," finding the predicted sex difference in the nature of the onscreen interrogations (that males focused on the sexual aspects of the purported infidelity, whereas females focused on the emotional aspects).

In sum, fewer studies have examined the sex difference in jealousy using retrospective reports of actual infidelity experiences than using responses to hypothetical infidelity scenarios, and these studies have produced mixed results, with some (Berman & Frazier, 2005; Harris, 2002; Zengel et al., 2013, continuous measures) not finding evidence of sex differences but others (Edlund et al., 2006; Zengel et al., 2013, forced-choice measure) finding evidence of sex differences. Sagarin et al.'s (2012) meta-analysis of continuous-measure studies found a significant overall effect, but this was across only seven studies.

Is Automaticity Relevant?

Social psychology has long approached conscious responses as only part of the equation—nonconscious processes have long been considered important to the study of psychological phenomena. This idea has also been applied to the study of the sex difference in jealousy in a number of different ways.

The first study that explored the automaticity issue was DeSteno et al. (2002). In this paper, DeSteno et al. first tested the sex difference in jealousy using both forced choice and continuous measures and replicated the sex difference in jealousy only on the forced-choice measure (see earlier section on psychometric issues for a more extensive review of this study). In their next study, DeSteno and colleagues placed some participants under cognitive load and found that the sex difference disappeared under cognitive load.

The results found by DeSteno et al. (2002) have been used to suggest that the sex difference in jealousy is simply an artifact of measurement, because, as DeSteno et al. argued, an evolved mechanism should be automatic. However, there have been a number of concerns raised by researchers in response to DeSteno et al. (2002). Feldman Barrett et al. (2006) challenged DeSteno et al.'s underlying assumption that an evolved mechanism should be immune to any form of context or mental resource challenge. Edlund and Sagarin (2009) and Sagarin et al. (2012) have argued that social norms, available mental resources, and any of a number of other factors could impact the observed reactions of participants to infidelity scenarios. Other researchers have more directly questioned the methodology used by DeSteno et al. (2002) and the lack of counterbalancing of conditions and responses. For instance, when response order

is controlled through counterbalancing, the expected sex difference in jealousy effect emerges (Schutzwohl, 2008a). Finally, Sagarin (2005) reanalyzed DeSteno et al.'s data, finding that the cognitive load attenuated but did not eliminate the effect.

In a similar vein, Schutzwohl (2008b) explored how well participants could disengage from various cues (a proxy for how much attention these cues were taking from available cognitive resources). Schutzwohl found that men had significantly more difficulty disengaging from sexually related cues (e.g., you notice that your partner seems bored when you have sex), whereas women had significantly more difficulty disengaging from emotionally related cues (e.g., your partner doesn't respond anymore when you tell him that you love him).

Additional studies have explored the cognitive manifestations of the sex difference in jealousy in a few other ways. For instance, Schutzwohl (2006) explored what kinds of information people seek with regard to a partner's infidelity. Schutzwohl found that men sought more information related to the sexual components of a partner's potential infidelity, whereas women sought more information related to the emotional components of a partner's infidelity. Other studies have dealt with how quickly men and women reach thresholds for jealousy. Schutzwohl (2005) found that there was no difference in how quickly men and women reach the threshold for the first pangs of jealousy. However, once the threshold had been reached, men reacted much more powerfully to cues to sexual infidelity (needing fewer sexual cues to react a point where the jealousy would be unbearable), whereas women reacted much more powerfully to cues to emotional infidelity (needing fewer emotional infidelity cues to reach a point where the jealousy would be unbearable).

Finally, researchers have explored other sex differences in jealousy using implicit measures. For instance, Maner et al. (2009) explored what targets would elicit the most jealousy in participants using implicit measures of attention. Maner et al. found that attractive same-sex rivals captured the most cognitive attention of the participants and that the sex of the participant moderated the responses, where women showed a significantly larger response to the attractiveness manipulation. Although Maner et al. did not test the theory of evolved sex differences in jealousy directly, their methods could be applied to research in this area.

Physiological Manifestations

Study 2 of Buss et al. (1992) collected measures of physiological arousal (specifically measures of electrodermal activity, EDA; pulse rate, PR; and

electromyographic, EMG, activity) when participants imagined sexual infidelity and emotional infidelity. Using these measures, the researchers found that men had significantly higher EDA and PR activity in response to the sexual infidelity scenario (compared to the emotional infidelity scenario) and women showed higher EDA in response to the emotional infidelity scenario (compared to the sexual infidelity scenario). Based on this evidence, Buss and colleagues concluded that the physiological measures showed converging evidence of an evolved predisposition to certain jealousy triggers.

Mixed results on physiological measures have been seen in other studies. Grice and Seely (2000) investigated the sex difference in jealousy using the same measures as Buss et al. Grice and Seely found support for the theory when using the PR measure; results for the EDA ran counter to the results found by Buss et al. (where women showed a marginally significant increase in response to the sexual items); the EMG measure did not result in any difference between men and women. Pietrzak et al. (2002) measured four physiological responses (EDA, EMG, PR, and skin temperature) while participants engaged in three imagery tasks: neutral imagery, sexual infidelity imagery, and emotional infidelity imagery. Pietrzak et al. found significant theory-supportive effects across all four measures for both men and women. Harris (2000), on the other hand, used similar measures (PR, systolic blood pressure, diastolic blood pressure, and EDA) and failed to find theory-supportive effects.

Another study (Takahashi et al., 2006) attempted to move beyond EDA, PR, and EMG methodologies and instead looked at brain activity directly using functional magnetic resonance imaging (fMRI). In this study, participants completed self-report measures of jealousy (featuring sexual infidelity, emotional infidelity, as well as a neutral condition) and had their brains scanned during imagery activities dealing with infidelity. The self-report methodology did not result in a significant sex difference (and, given the small sample size, this is unsurprising). However, when brain activation was analyzed, there were differences between men's and women's responses to the jealousy situations. Specifically, men showed greater activation in the amygdala and the hypothalamus (which is thought to tie into reproductive behavior: Sisk & Foster, 2004), whereas women showed greater activation in the posterior superior temporal sulcus (which has been shown to relate to detection of deception, Calarge et al., 2003, and violations of social norms, Takahashi et al, 2004).

A subsequent study, Baschnagel and Edlund (2016), was designed to address a number of Harris's (2000; 2005) critiques. Baschnagel and Edlund asked participants to respond to jealousy-provoking scenarios that dealt with emotional and sexual infidelity using continuous measures of jealousy while collecting

physiological data using affective modification of the startle eyeblink. Baschnagel and Edlund also included a number of control items designed to allow the researchers to statistically control for men's greater response to sexually related items more generally. Baschnagel and Edlund found a marginally significant (p = .051) interaction between sex and imagery type such that men showed a greater response to sexual infidelity items (compared to the emotional infidelity items and the sexuality control items) on the startle eyeblink measure. Women had a much smaller mean difference in the startle eyeblink with slightly larger startle responses to the emotional infidelity items (p >.10).

Meta-analyses

In 2003, Harris published the first meta-analysis on sex differences in jealousy as part of a critical review of the literature. Harris meta-analyzed forced-choice responses from thirty-two independent samples. As Harris reported, almost all of the studies used one or both of the two questions from Study 1 of Buss et al. (1992), most in the exact form, some with slight wording changes. Harris found a significant overall effect across samples. This effect was significantly moderated by sexual orientation, with heterosexual participants showing a stronger sex difference than gay and lesbian participants The effect was also significantly moderated by the age of the sample (college students displaying large effect).

Nine years later, Carpenter (2012) and Sagarin et al. (2012) published meta-analyses of the literature on sex differences in jealousy, seemingly reaching opposite conclusions. Carpenter meta-analyzed 172 effect sizes from fifty-four articles, examining responses to both forced choice and continuous measures, concluding that there was no evidence for the sex difference in jealousy. Sagarin et al. meta-analyzed 209 effect sizes from forty articles, examining responses only to continuous measures concluding that the sex difference in jealousy was a real effect.

These opposite conclusions were not based on differing statistical results—the statistical results themselves were quite consistent across both meta-analyses. The critical difference was the interpretation of the results. Carpenter (2012) based his conclusions on the simple effect of infidelity type within each sex. Based on the findings that (1) both men and women tended to choose the emotional infidelity as more distressing on forced-choice measures, and (2) both men and women tended to rate the sexual infidelity as more jealousy provoking on continuous measures, Carpenter concluded that the data support the social-cognitive perspective rather than the evolutionary psychology perspective.

Sagarin et al. (2012) based their conclusions, instead, on the participant sex by infidelity type of interaction that was significant. Thus, Sagarin et al. concluded that the data support the theory of evolved sex differences in jealousy. Carpenter (2012) also noted that his data also showed this pattern of interaction, although he argued it was irrelevant.

Carpenter (2012) and Sagarin et al. (2012) also identified a number of moderators of the sex difference in jealousy. Consistent with Harris (2003), Carpenter found that lesbian and gay respondents tended to show smaller or reversed patterns of responses on forced-choice measures compared to heterosexual respondents. Carpenter also found cultural differences on forced-choice measures, such that men outside the United States tended to choose the emotional infidelity as causing greater distress, whereas men within the United States tended to choose the sexual infidelity as causing greater distress. Finally, Carpenter found that scenarios that precluded a double-shot interpretation (DeSteno & Salovey, 1996) tended to show smaller sex differences compared to scenarios that allowed for a double-shot interpretation, suggesting that the double-shot hypothesis might explain some, but not all, of the sex difference in jealousy. Sagarin et al. (2012) also found evidence for moderation, such that the emotional term moderated the effect (with jealousy and distress/upset yielding the largest results). They also found evidence for six other moderators: random sampling, population type (student vs. nonstudent samples), age, inclusion of a forced-choice question, number of points in the response scale, and year of publication.

Sexual Orientation and the Sex Difference in Jealousy

As the meta-analyses by Carpenter (2012) and Harris (2003) demonstrated, the sex difference in jealousy has proven quite robust when measured using forced-choice infidelity dilemmas. There is, however, one moderator that consistently attenuates or even reverses the sex difference: sexual orientation. As noted earlier, in Harris's meta-analysis, heterosexual participants showed a stronger sex difference than gay and lesbian participants. Likewise, Bailey et al. (1994) reported significant sex differences in jealousy among heterosexual women and men, but no sex differences in jealousy among lesbians and gay men.

Sexual orientation has also been examined in the relationship between the unfaithful partner and the rival. Sagarin et al. (2003) presented heterosexual participants with a forced-choice infidelity dilemma in which their opposite-sex partner had become interested in a rival of either the opposite sex or the same

sex. Participants considering a rival of the opposite sex as the partner showed the typical sex difference in jealousy, with significantly more men than women choosing the sexual infidelity as more distressing. Participants considering a rival of the same sex as the partner showed no sex difference in jealousy.

In an attempt to account for the finding that the sex difference in jealousy tends to disappear among lesbians and gay men as well as among heterosexual women and men contemplating their opposite-sex partners becoming involved with a rival of the same sex as the partner, Sagarin et al. (2012) offered "a reproductive threat-based model of evolved sex differences in jealousy that predicts that the sexes will differ only when the jealous perceivers' reproductive outcomes are differentially at risk" (p. 487).

Consistent with the reproductive threat-based model of evolved sex differences in jealousy, the sex difference in jealousy emerged only among heterosexual women and men contemplating an opposite-sex infidelity. Heterosexual women and men contemplating a same-sex infidelity, and lesbians and gay men contemplating either an opposite-sex infidelity or a same-sex infidelity showed no sex difference.

Scherer et al. (2013) tested the model with a sample of bisexual women and men. Participants reported whether they were currently dating a man or a woman and responded to the first forced-choice infidelity question from Study 1 of Buss et al. (1992). Consistent with the reproductive threat-based model of evolved sex differences in jealousy, bisexual men dating women and bisexual women dating men showed a significant sex difference in jealousy, but bisexual men dating men and bisexual women dating women showed no sex difference.

A study done by Frederick and Fales (2016) also sought to address the sex difference in jealousy taking into consideration relationships outside simply heterosexual relationships. For heterosexual participants, traditional sex differences were seen. Women were more likely to be distressed by the thought of emotional cheating whereas men were more likely to be distressed by the thought of a sexual infidelity. Apart from heterosexuals, however, there was no significant difference between sex of the participant and the form of infidelity chosen as most distressing.

Other Moderators of the Sex Difference in Jealousy

In addition to sexual orientation, researchers have proposed and tested a number of other moderators of the sex difference in jealousy. These include relationship experience (Buss et al., 1992); relationship status (Becker, et al., 2004); infidelity experience (Sagarin et al., 2003; Tagler, 2010); mate value

(Edlund & Sagarin, 2014; Edlund et al., 2018); demographic variables (Zengel et al., 2013); attachment style (Brase et al., 2014; Levy & Kelly, 2010; Güçlü et al., 2017); sex roles; sociosexual orientation, trust, and beliefs (Brase et al., 2014); type of emotion (Sagarin et al., 2012); and sociocultural variables (Canto et al., 2017).

Buss et al. (1992) theorized that experience in romantic relationships would increase men's jealousy in response to sexual infidelity and women's jealousy in response to emotional infidelity. Women showed a small, nonsignificant difference in their choice of which type of infidelity caused greater distress based on relationship experience. Men, in contrast, were significantly more likely to choose the sexual infidelity as causing greater distress if they had been in a committed sexual relationship (compared to men who had not been in a committed sexual relationship). Becker et al. (2004) found that participants in a committed relationship reported more intense reactions to both sexual infidelity and emotional infidelity compared to participants who were casually dating and participants who were not in a relationship.

Edlund and Sagarin (2014) examined mate value as a possible moderator. They found that mate value significantly moderated the sex difference in jealousy, such that participants higher in mate value showed a stronger sex difference in jealousy in the theory-consistent direction. This finding was replicated by Edlund et al. (2018) who saw this pattern in a wider variety of samples.

Zengel et al. (2013) examined sex differences in jealousy as part of a large survey conducted on a representative sample of American adults. The survey included a number of demographic variables. Sex differences in jealousy emerged on the forced-choice measures but not on the continuous measure. The sex difference in jealousy in response to hypothetical infidelity scenarios, in contrast, was moderated by a number of demographic variables including "household size, the number of adult household members, the presence of children between the age of 2–5, household income, status of being the head of the household, and the ownership status of the living quarters" (p. 49).

Levy and Kelly (2010) examined attachment style as a possible moderator of sex differences in jealousy. Participants responded to the first question of Study 1 of Buss et al. (1992) and indicated their attachment style on Bartholomew and Horowitz's (1991) Relationship Questionnaire. Participants with fearful and dismissing attachment styles showed significant sex differences in jealousy, but participants with secure and preoccupied attachment styles showed nonsignificant sex differences. Brase et al. (2014) also examined attachment style as a possible moderator; despite finding significant sex differences in

jealousy on all of their forced-choice measures, they found no significant participant sex by attachment style interaction. Güçlü et al. (2017) similarly sought to understand the influence of attachment styles on jealousy. Looking at a number of married couples, Güçlü et al. were able to find that ambivalent attachment lead to higher rates of various responses to jealousy. As such, given the discrepant results, it is unclear whether attachment style does indeed moderate responses.

Brase et al. (2014) tested a number of potential moderators beyond attachment style (Sex Roles, Male Roles, Attitudes toward Women, Trust, Sociosexual Orientation, and Culture of Honor Scale) in a regression equation that included participant sex, the moderators, and the interactions between participant sex and each of the moderators. No significant interactions emerged, suggesting that these variables do not moderate the sex difference in jealousy when all variables are tested simultaneously.

A number of studies have measured men's and women's responses to sexual infidelity and emotional infidelity across a variety of emotions, sometimes (but not always) including jealousy (e.g., Becker et al., 2005; Geary et al., 1995; Shackelford et al., 2000). Results have typically demonstrated differences across different emotions. As noted earlier, Sagarin et al. (2012) examined emotion as a possible moderator meta-analytically, finding that the sex difference was strongest for distress/upset and jealousy and weaker for other negative emotions.

Finally, sociocultural variables were found to play a role in which form of infidelity proved to be the most distressing. By looking at a group of Portuguese and Brazilian participants, Canto et al. (2017) found that culture of honor as well as the masculinity or femininity of the individual played a role in what infidelity caused the most distress. "Honor codes define a pattern of inter-sex-relations that have implications for attitudes towards sex roles" (Canto et al., 2017). For males in particular, being able to provide for and protect their family are key components of this code of honor. Women on the other hand, according to the honor code are to be modest and submissive to their partner. It was found that men displayed higher scores aligning with their culture of honor. In sum, men were more likely to align with the masculine attributes according to the honor code. Scoring highly in either masculine or feminine attributes as well as aligning with the culture of honor played a role in overall ratings of distress regarding infidelity; those with higher scores were more likely to have a form of jealousy aligning with their gender (males—sexual, females—emotional). The authors note, however, that in all, both men and women were seen to have higher distress caused by emotional infidelity.

Where the Debate Stands

Having looked back at twenty-eight years of work on the sex difference in jealousy, we can conclude with confidence that there are meaningful differences between men and women in terms of how they experience jealousy in romantic relationships. The strongest support has come from studies using the forced-choice hypothetical infidelity dilemmas pioneered by Buss et al. (1992). Meta-analyses by Harris (2003) and Carpenter (2012) have found that, when faced with a choice of which type of infidelity (sexual vs. emotional) would cause greater distress, men consistently choose the sexual infidelity more often than do women. Strong support has also come from studies using continuous measures to assess responses to hypothetical infidelities. Although individual studies sometimes fail to produce a significant sex difference, a meta-analysis by Sagarin et al. (2012) found a highly significant overall effect across continuous measure studies. Buss and Haselton (2005) identified thirteen empirically supported sex differences consistent with the existence of evolved sex differences in jealousy including sex-differentiated patterns of rival characteristics that provoke greater distress and mate guarding. Finally, some support has come from creative methodologies that extend beyond the self-report, including cognitive effects identified by Schutzwohl (2005, 2006, 2008a, 2008b) and an analysis of reality television conducted by Kuhle (2011).

Although a number of challenges have been addressed (e.g., DeSteno & Salovey, 1996, double-shot hypothesis; DeSteno et al., 2002, concerns regarding continuous measures; Harris, 2002, concerns regarding responses to actual infidelity experiences), others remain unanswered (e.g., Kato, 2014, alternative explanation based on men's greater tendency than women's toward vivid sexual imagery) or only partially answered (e.g., Harris, 2000, alternative explanation based on men's greater physiological reactivity than women's in response to sexual imagery). Edlund et al. (2019) also offered an alternative explanation for male sexual jealousy. Contrary to the widely used explanations for the sex difference in jealousy, Edlund et al. (2019) found that threats to paternity opportunities (as opposed to paternal uncertainty) appear to be the root of the jealousy response. With this explanation only adding to the debate, it is clear that there is much work that remains to be done, in order to more fully understand sex differences in jealousy. We believe that researchers should continue to investigate moderators of the sex difference in jealousy, expand the work looking at physiological manifestations of the jealousy, develop methodologies to examine real-time experiences of jealousy, further explore the theoretical underpinnings of the sex difference in jealousy, and consider how cross-cultural

variability impacts the effect and what this means for the underlying theory.

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CHAPTER 20

Mate Guarding

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Abstract

Mate guarding includes behaviors that function to reduce the likelihood of a partner's defection from an ongoing long-term relationship. Some mate-guarding behaviors function by enticing a current partner's continued investment in the relationship through the provision of gifts or other benefits. Other mate-guarding behaviors function by removing a partner's alternatives to the ongoing relationship through subjugation or violence and the infliction of costs sufficient to remove a partner's ability to defect from the relationship. Mate-guarding behaviors represent evolved responses to the costs of losing a long-term partner. However, as the potential benefits of relationship defection persist despite a partner's guarding, there is an arms race between attempts to maintain the opportunities afforded by extra-pair relationships and a partner's attempts to thwart those opportunities and avoid the costs of that defection.

Key Words: mate guarding, mate retention, mating strategies, relationship dissolution, relationship defection

Mate-guarding behaviors are intended to thwart an intimate partner's defection from a long-term relationship. Mate-guarding behaviors are produced by adaptations that evolved as a consequence of sexual conflict associated with the costs and benefits of humans' pursuit of two distinct mating strategies. As a socially monogamous species, humans can and do employ both short-term and long-term mating strategies, with motivations encouraging one strategy or the other being moderated by a range of individual difference and circumstantial variables (Buss, 2006). Perhaps most influential in the selection of a mating

strategy is the quantity of obligate parental investment, which is profoundly sexually dimorphic in humans and many other species (Trivers, 1972). That is, to successfully reproduce, females more than males are burdened with the heavy costs of gestation, birth, and lactation, and the limitations these costs impose on potential alternative mating opportunities. Consequently, females are often disproportionately motivated to pursue a long-term strategy in which sexual access is granted primarily to those males who are willing and able to commit to and invest in her and any offspring she produces.

Unlike females, males are not particularly limited by their own reproductive biology. Sperm are metabolically inexpensive (Hayward & Gillooly, 2011) and a male's minimum parental investment can end with the comparatively minuscule amount of energy (Frappier et al., 2013) required to place sperm in a female's reproductive tract. And as this leaves males free to immediately pursue additional mating opportunities, males are less motivated to restrict their mating behaviors to the confines of a long-term strategy. However, that a male is motivated to pursue a short-term strategy does not guarantee that he will be successful in finding females with which to pursue such a strategy. As females are more likely to restrict sexual access to long-term partners, males can often gain sexual access to a partner, particularly one of comparatively high value, who would not otherwise proffer it by agreeing to the confines of a long-term mating strategy. A long-term strategy can also increase males' paternity certainty and overall reproductive success, in addition to providing an avenue for increased social status and alliance formation (Buss, 2019). In other words, albeit for different reasons, both males and females can benefit from a long-term mating strategy.

This is not to suggest that a long-term strategy is necessarily the more valuable strategy for human mating. Both females and males can benefit from engaging in a short-term strategy—either instead of or in addition to a long-term strategy—under particular contexts and circumstances. For males, the "right" circumstance is often simply one of opportunity. Males who can engage in a short-term strategy are likely to do so (Clark & Hatfield, 1989; Schützwohl et al., 2009). Females, on the other hand, pursue a short-term strategy only when the potential partner is of particularly high mate value (Schützwohl et al., 2009), thus rendering the high potential costs of reproduction worthwhile.

Ultimately, there are potential benefits to both males and females for pursuing either a short-term mating strategy or a long-term mating strategy. These benefits, however, are not mutually exclusive. One can gain the benefits of a long-term strategy while simultaneously pursuing the benefits gained by a short-term strategy. That is, people may supplement their long-term relationships with

short-term extra-pair partnerships (Buss & Shackelford, 1997b; Shackelford et al., 2008; Starratt et al., 2017). For males, this supplementation can result in access to a greater number of sexual partners, which can increase males' total reproductive success. For females, extra-pair partnerships may provide two benefits. For one, as females choose as extra-pair partners specifically those males who are of higher genetic value than their current long-term partner (Gangestad & Simpson, 2000; Scheib, 2001), they may secure social and material resources from a long-term partner while securing "better" genes from a different short-term partner. A second potential benefit of an extra-pair partnership for females is the opportunity to trade-up or switch mates (Buss et al., 2017; Drigotas & Barta, 2001), whereby an extra-pair partnership may lead to dissolution of the current long-term relationship in favor of a new long-term relationship with the higher value "previously extra-pair but now current" long-term partner. This is more likely to occur when a woman is of higher mate value than her original long-term-partner (Moran et al., 2017).

As there are benefits to engaging in a long-term mating strategy and benefits to straying from that long-term relationship, people who engage in a long-term mating strategy are at risk of their partners' defection. Consequently, males and females have evolved motivations to engage in an array of mate-guarding behaviors as an evolved response to the potential costs of a partner's defection from a long-term relationship.

Mate-Guarding Function and Form

Mate-guarding behaviors include those behaviors that function to reduce the likelihood of a partner's defection from the current long-term relationship (Buss & Shackelford, 1997a). Although there are many different specific behaviors that function to guard a mate, they can be divided into two broad categories: benefit-provisioning behaviors and cost-inflicting behaviors (Miner et al., 2009).

Benefit-provisioning mate-guarding behaviors function by enticing a partner's continued investment in the long-term relationship. Some of these benefit-provisioning mate-guarding behaviors accomplish this by increasing relationship satisfaction, which can be a valuable defection deterrent as indicated by the negative correlation between relationship satisfaction and likelihood of relationship defection (Mark et al., 2011; Shackelford et al., 2008). The more satisfying one finds a current relationship to be, the less likely one is to seek out alternatives to that relationship. The ways in which one might increase a partner's relationship satisfaction vary and can include behaviors such as promoting oneself as a supportive and empathetic partner (Cramer & Jowett,

2010) to behaviors that bestow sexual benefits, such as performing oral sex on a partner (Pham & Shackelford, 2013; Sela et al., 2015). Regardless of the mode or method of benefit bestowal, a partner who is satisfied in the current relationship is a partner who is less likely to defect from that relationship.

Other benefit-provisioning mate-guarding behaviors function by highlighting or increasing one's own value as a mate. This can be an effective defection deterrent given that people may be less likely to risk losing a partner they perceive to be particularly attractive or valuable (Starratt et al., 2017). Again, the ways in which one can attempt to increase value or attractiveness as a mate vary and differ by sex. For example, men may find particular value in increasing their perceived attractiveness through display of wealth (Wang et al., 2018) or generosity (Van Vugt & Iredale, 2013). The accumulation of resources and the willingness to invest those resources in a partner are high mate value traits in men (Buss, 1989), and men with these traits are perceived to be more attractive and, therefore, may be less likely to suffer a partner's defection. Women, on the other hand, may be better served by enhancing their physical appearance. These enhancements could be temporary and superficial, such as accomplished through choice of clothing (Elliot & Niesta, 2008), or more drastic and long-lasting, such as accomplished by cosmetic surgery (Atari et al., 2017). Whatever the method of appearance enhancement, however, the consequence in terms of mate guarding is the same—reducing a partner's likelihood of defecting from the relationship by making oneself too attractive to risk losing.

On the opposite end of the mate-guarding spectrum are cost-inflicting mate-guarding behaviors. This class of behaviors function not by enticing a partner's continued investment but by reducing a partner's actual or perceived alternative mating opportunities or by punishing or threatening to punish a partner's defection from the current long-term relationship. Some of these cost-inflicting behaviors are relatively mild, such as engaging in deceptively affectionate behaviors in which the level of affection demonstrated exceeds the actual level of affection (Caton & Horan, 2019). Although not imposing a direct cost, deceptive affection can dissuade an individual from recognizing the risks of continuing to invest in a relationship in which they are more invested than their partner.

Another class of cost-inflicting mate-guarding behaviors includes partner-directed insults (McKibbin et al., 2007; Starratt et al., 2008). It may seem counterintuitive to attempt to retain a partner by insulting them. However, insulting a partner serves the purpose of reducing that partner's perception of their own value. By reducing a partner's perceived mate value, one is effectively reducing that individual's perceived alternatives to the current relationship. For

example, some partner-directed insults include derogations of a partner's physical attractiveness or derogations of a partner's value as a person or partner (Goetz et al., 2006). If such derogations were accurate, they would indicate that the individual is of quite low value as a partner. As a person of such apparently low value is unlikely to be able to successfully entice anyone else into a relationship, there would be no reason to risk leaving the current relationship. Thus, one could effectively guard against a partner's defection by insulting that partner into believing that no one else would have them and so their only course of action is to remain invested in the current relationship, provided that the partner's self-perception was not protected from devaluation by competing bolstering from elsewhere.

In addition to reducing the perceived available alternatives to the current relationship, one might also effectively reduce the number of actual opportunities a partner would have to defect from the current relationship. This could be accomplished through either direct guarding or competitor derogation and violence against rivals (Buss & Shackelford, 1997a). That is, a person could guard their mate simply by cloistering them from potential alternative mates, such as by refusing to allow them to be in the physical presence of other people at parties or other social events. Alternatively, an individual could focus their attention on the intrasexual rival, and engage in or threaten violence against a person who might provide a partner with an alternative mating opportunity. If one's partner is not permitted to be around other people, or if those other people are effectively dissuaded from perceiving one's partner as a potential target for poaching (Starratt & Shackelford, 2010), a partner's alternatives to the current relationship are functionally diminished and the risk of defection is reduced.

Sometimes, aggressive and violent cost-inflicting mate-guarding behaviors are directed not toward one's rival but toward one's partner. (Goetz et al., 2008). In fact, it has been argued that female-directed intimate partner violence functions as a cost-inflicting mate-guarding behavior by punishing or threatening to punish a partner's potential defection (Buss & Duntley, 2011; Kaighobadi et al., 2008; Shackelford et al., 2005). That is, a person who is threatened or physically assaulted for talking to, looking at, or even ostensibly thinking about someone other than their current partner may be less likely to successfully defect from the current relationship. It is worth noting that, odious as these cost-inflicting behaviors may be, similar types of mate-guarding techniques are common across many species, from some of humans' closest relatives, like chimpanzees (Watts, 1998), to more distant cousins, such as the fruit fly (Baxter et al., 2015).

When Do People Mate Guard?

Of course, functional though the behaviors may be, not all people engage in mate guarding at all times. The extent to which people engage in mate guarding is moderated by a range of individual differences and circumstantial variables. Generally, though, for both men and women, motivation to engage in mate guarding is greatest when the stakes are highest. That is, people are more likely to deploy mate-guarding behaviors when the risk of mate defection is higher and when the cost of losing that mate is higher.

For men, many of these cost-inflicting mate-guarding behaviors are inextricably linked to the relationship between a female partner's brief relationship defection and the risk of sperm competition and cuckoldry (Shackelford et al., 2006; Shackelford et al., 2007). As cuckoldry has been a recurrent adaptive problem for men, men have evolved a host of anticuckoldry tactics, which include mate-guarding behaviors (Goetz et al., 2007; Shackelford & Goetz, 2007). Consequently, males' likelihood of deploying mate-guarding behaviors is positively associated with the risk of partner infidelity and cuckoldry. This pattern persists when assessing risk of partner infidelity and cuckoldry in terms of increased extra-pair opportunity given time spent apart from one's partner (Starratt et al., 2007), increased fertility due to ovulatory status (Gangestad et al., 2002; Pillsworth & Haselton, 2006), lower levels of relationship commitment (French et al., 2017), or even increased perceived female sexual receptivity as suggested by her clothing choice (Prokop & Pazda, 2016). In short, as the possibilities that a female partner has been presented with or taken advantage of an extra-pair mating opportunity and become pregnant by such opportunity increase, the likelihood of her partner deploying in mate-guarding behaviors also increases.

Risk of partner defection is influenced not only by the states, traits, and behaviors of one's partner but also by the presence and quality of one's partner's potential alternatives to the current relationship. For example, women who are fertile and perceive their current long-term male partners to be less sexually attractive are more interested in engaging in extrapair sexual behavior (Buss et al., 2017) and are consequently more likely to be the targets of benefit-provisioning mate-retention behaviors from their long-term partners (Pillsworth & Haselton, 2006). Similarly, a woman is more likely to guard her male partner when the pair is around other fertile females (Hurst et al., 2017). This is likely because although women are more likely to engage in extra-pair partnerships which could result in "trading up," men are more likely to engage in an infidelity when provided the opportunity (Starratt et al., 2017), and the presence of fertile

women indicates extra-pair opportunity for men. In either case, however, as the apparent availability of extra-pair partnerships increases, so too does a partner's deployment of mate-guarding behaviors.

Just as a partner's apparent extra-pair opportunities affects one's engagement in mate-guarding behavior, one's own opportunities are similarly influential. The difference is that one's engagement in mate guarding is increased by an increase in one's partner's available alternatives, but it is similarly increased by a *decrease* in one's own available alternatives. That is, one is more likely to guard against losing a partner when there are fewer opportunities to secure alternative partners. If it does not appear that alternatives abound for oneself, more effort is devoted to maintaining a current partner's investment in the ongoing relationship, which translates to an increase in the performance of mate-guarding behaviors (Arnocky et al., 2014).

Who Is More Likely to Mate Guard?

Although there are certain circumstances in which people are more likely to engage in mate guarding, there are also some people who are more likely to deploy mate-guarding behaviors than are other people. Some people are unlikely to deploy any mate-guarding behaviors, while other people deploy mate-guarding behaviors judiciously such that they favor the provision of benefits over the inflicting of costs, and still others engage in both benefit-provisioning and cost-inflicting mate-guarding behaviors (Lopes & Shackelford, 2019). The individual difference variables associated with an increased likelihood of engaging in mate-guarding behaviors are those that are associated with an increased cost of a partner's defection and thus an increased advantage to guarding that partner.

For example, people who share biological children with their long-term partner are more likely to guard that partner than are people who do not share children with their long-term partner (Barbaro et al., 2016). Given the value of biparental care and the associated greater costs of losing the partner with whom one shares offspring and parental duties, the motivation to guard against that loss is comparatively high. The cost of the loss of a partner is also high when that partner is of high mate value. Consequently, there is also an increase in mate-guarding behaviors, particularly benefit-provisioning mate-guarding behaviors, by men whose partners are of comparatively high value (Starratt & Shackelford, 2012). This positive relationship between benefit-provisioning mate guarding and mate value extends to own value in addition to a partner's value. That is, there is a relative increase in the deployment of benefit-provisioning mate-

guarding behaviors by men who themselves are of relatively high mate value (Miner et al., 2009a; Miner et al., 2009b). The source of this particular relationship between mate value and mate guarding may be twofold. First, benefit-provisioning mate-guarding behaviors are likely to be less risky than cost-inflicting mate-guarding behaviors in that they are more likely to evoke positive rather than negative regard. Second, a person who is of high value may be in a better position to be able to afford the material or psychosocial costs of provisioning their partner with benefits.

The flip side of higher value males' deployment of benefit-provisioning mate-guarding behaviors is lower mate value males' deployment of cost-inflicting mate-guarding behaviors (Daly & Wilson, 1988; Miner et al., 2009b). This, however, is not the only individual difference trait associated with deployment of cost-inflicting mate-guarding behaviors. For example, individuals who score higher on Machiavellianism, a trait associated with a willingness to manipulate others for personal gain, are more likely to engage in a range of cost-inflicting mate-guarding behaviors. This includes behaviors directed at one's partner—such as those that reduce a partner's access to potential alternative mates—as well as behaviors directed at rivals who might tempt a partner to defect from the ongoing long-term relationship (Brewer & Abell, 2015).

There is even emerging evidence linking individual differences in the deployment of mate-guarding behaviors to the physiological mechanisms underlying the motivations to engage in such behavior. For example, individual differences in copy number variations of the androgen receptor gene, which influences the phenotypic effects of androgens, has been associated with individual differences in responses to a partner's potential relationship defection (Lewis et al,, 2016). Specifically, longer versions of the androgen receptor gene have been associated with greater sexual jealousy and greater attention to and motivation to "correct" partner infidelity. While the nature of the gene-behavior relationship is not yet clear, the relationship is consistent with existing behavioral and psychosocial evidence, particularly given that such longer versions of the androgen receptor gene are associated with reduced phenotypic masculinization and, consequently, less of those traits that women find attractive in a mate, including upper body strength and social prestige (Simmons & Roney, 2011). In other words, men with longer androgen receptor gene alleles are less masculine, have physical and psychosocial traits associated with lower mate value, and have cognitive tendencies that make them more prone to engage in mate guarding behaviors.

Resistance to Mate Guarding

Although mate guarding evolved to address the adaptive problem of a partner's defection from a long-term relationship, the existence of a partner's mate guarding does not summarily extinguish the potential value of the defection from which the partner guards themselves. Even with the potential negative consequences of a partner's guarding behavior, there exist the potential benefits of defection. Consequently, people may be motivated to resist a partner's mate-guarding efforts (Cousins et al., 2015). This arms race between a person's motivation to engage in extra-pair mating and a partner's motivation to deploy mate-guarding behaviors is evident in the fact that the same circumstances are linked to an increase in both the need for mate guarding and the need to resist mate guarding. The same variables associated with an increase in mate guarding appear to be associated with an increase in resistance to that guarding, at least among women. This is not to suggest that men do not similarly resist a partner's guarding attempts, which they likely do, but to the best of our knowledge current evidence seems restricted to research on women's resistance efforts.

Just as a person is most likely to engage in mate guarding when their partner's extra-pair mating opportunities are relatively abundant, that partner is more likely to resist mate guarding when retaining access to extra-pair mating opportunities is comparatively high. Specifically, for example, women who perceive themselves to be more attractive than their partner are more likely to engage in resistance to mate-guarding behaviors (Fugere et al., 2015). This is because a woman who is more attractive than her partner and allows herself to be successfully guarded against defection effectively loses any potential opportunity to trade up and leave her current partner in favor of a new partner of higher value. Resisting a partner's mate-guarding behaviors, then, may help to preserve those trade-up opportunities.

Trading up is not the only potential benefit of defection, however, and so is not the only time when resistance to mate-guarding behaviors is greater. Women can benefit from defection by supplementing the material resources they get from a long-term partner with genetic resources from an extra-pair partner. Consequently, women may benefit from maintaining extra-pair opportunities when they are most fertile and, therefore, engage in greater resistance to a partner's mate-guarding behaviors when they are most fertile (Gangestad et al., 2014).

Additionally, just as one who scores high on Machiavellianism is more likely to deploy mate-guarding behaviors, one who scores high on Machiavellianism is similarly likely to engage in resistance to a partner's mate-guarding behaviors,

thus retaining access to potentially beneficial alternative mates (Abell & Brewer, 2016). This relationship between Machiavellianism and mate guarding highlights the functions of mate guarding and the resistance to mate guarding. People are motivated to engage in behaviors that are most beneficial to themselves—such as maintaining the ability to secure the advantages of both a long-term mating strategy and a short-term mating strategy simultaneously—while preventing their own partner from doing the same.

The Evolution of Mate GuardingAs a socially monogamous species, humans have evolved motivations to pursue both a long-term mating strategy and a short-term mating strategy under the right conditions. This creates conflict, in which the value to a person of defecting from a long-term relationship—either briefly or completely—is detrimental to that person's long-term partner. Therefore, people have evolved motivations to engage in mate-guarding behaviors. Although varying widely, mate-guarding behaviors can be categorized as benefit provisioning or cost inflicting, with the former functioning by enticing a partner's continued investment in the current relationship and the latter functioning by reducing a partner's actual or perceived alternatives to the current relationship or punishing or threatening to punish a partner for failure to maintain investment in the current relationship. Of course, as mating opportunities outside the long-term relationship continue to be potentially valuable, people have evolved motivations to resist a partner's mate-guarding attempts. However, people do not indiscriminately deploy mate-guarding behaviors or resistance to mate-guarding behaviors. Instead, the likelihood of engaging in mate-guarding behaviors increases with the risks and consequences of a partner's relationship defection, whereas the likelihood of engaging in resistance to a partner's mate guarding increases with the value of maintaining an alternative mating strategy for oneself.

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PART V

Sexual Conflict in Mating

CHAPTER 21

Deception in Human Mating

Gayle Brewer

Abstract

Romantic and sexual relationships form an important part of the social landscape. These relationships are, however, vulnerable to deception with a range of evolutionary relevant consequences for each member of the relationship dyad (e.g., cuckoldry) and relationship (e.g., dissolution). The current chapter details the use of deception at each stage of romantic and sexual relationships. First is the use of deception to attract a partner and assist relationship formation, with particular emphasis on the falsification of sexual history. Reflecting recent mating trends, the chapter also considers the use of deception during online dating. Second, the chapter outlines deception within established relationships, including deceptive affection, pretending orgasm, and infidelity. Throughout, the chapter highlights important differences between men and women.

Key Words: deception, infidelity, online dating, pretending orgasm, sex differences

> "When one is in love, one always begins by deceiving one's self, and one always ends by deceiving others. That is what the world calls a romance."
>
> —Oscar Wilde (1891, p91)

Romantic and Sexual Relationships

Romantic and sexual relationships form an important part of the social landscape. In an evolutionary context, these relationships provide the framework for important life events and have a substantial impact on reproduction and survival relevant outcomes. Though men and women typically emphasize the

importance of honesty in romantic and sexual relationships, deception—defined as the creation of false or misleading impressions (Rowatt et al., 1998)—is widespread. There are, of course, a range of deception types. These include omission (i.e., withholding relevant information), distortion (i.e., manipulation through exaggeration), and contradiction (i.e., stating false information or denying the truth of accurate information) (Metts, 1989), and each occurs in the context of human mating.

Deception within romantic and sexual relationships may have a number of evolutionary advantages. These include access to high-quality mates who would reject the deceiver if provided with a more honest description and access to a large number of relationship partners including extra-pair relationships. If detected this deception may, of course, lead to a range of negative consequences including relationship conflict, reputational damage, and relationship dissolution (Aldeis & Afifi, 2015). This chapter details the use of deception at each stage of human mating. First, the chapter discusses deception to attract a partner and assist relationship formation, with particular emphasis on the falsification of sexual history. Reflecting recent mating trends, the use of deception during online dating is also considered. Second, the chapter outlines deception within established relationships, including pretending orgasm and infidelity.

Deception and Relationship Formation

> "Before marriage, a man declares that he would lay down his life to serve you; after marriage, he won't even lay down his newspaper to talk to you."
>
> —Helen Rowland cited in Buri (2006, p130)

The selection and attraction of a suitable sexual or romantic partner is of fundamental importance. It is unsurprising, therefore, that deception is often employed to gain advantage, for example, to appear more attractive and obtain otherwise unobtainable partners. The most important partner qualities and consequences of poor decision-making are, however, markedly different for men and women. Hence, the type of deception adopted by men and women and the motivation for such behavior is expected to reflect these evolutionary challenges. In particular, sex differences in human mating reflect the minimum levels of investment required by each sex to produce a healthy child and potential reproductive output.

The minimum investment required by men is low. Sperm are relatively "cheap" to produce, and men may choose to make no further investment in the woman or child after conception. Further, men are physically capable of

producing a large number of children and their reproductive output is restricted by his access to willing fertile partners rather than the capacity to conceive them. In contrast, women's fertility is more restricted, with menopause limiting later reproduction, and opportunities to become pregnant each month. If a woman does become pregnant, there is a minimum nine-month energy-intensive pregnancy, followed by an extended period of lactation. Therefore, reproductive output is more restricted than men's and from an evolutionary perspective, behavior intended to recruit support from partners and increase the well-being of each child is more beneficial than behavior attempting to increase the number of partners or children.

A substantial body of research has documented the manner in which these evolutionary pressures, including the minimum parental investment in each child, influences the type of relationship and relationship partner most preferred by each sex. According to the theory of parental investment (Trivers, 1972), the sex with the lower investment (i.e., men) should favor short-term relationships with fertile partners while the sex with the higher investment (i.e., women) should focus on long-term committed relationships with partners who are willing and able to provide supportive resources and care. Indeed, previous research indicates that, in general, men are more sexually promiscuous and women are more sexually cautious (Clark & Hatfield, 1989; Fletcher et al., 2014). Similarly, research (e.g., Buss & Schmitt, 1993; Kamble et al., 2014) indicates that men place a greater emphasis on the physical attractiveness of a partner, which provides a cue to her reproductive status and fertility, whereas women are more focused on the resources held by a potential mate and their willingness to share those resources with a relationship partner.

Each sex advertises a range of personal qualities in accordance with the aforementioned sex differences in partner preference. Such preferences also influence the use of deceptive advertising or false signaling. For example, both men and women report that men are more likely to lie about their resources (i.e., financial assets) or desire for a long-term relationship and falsify declarations of love (O'Sullivan, 2008). In contrast, women are more likely to conceal or alter their age, which is related to physical attractiveness and female fertility, in order to increase their access to high-quality partners (Pawlowski & Dunbar, 1999). Men and women are of course sensitive to deception as those believing false information are at risk of wasting time, emotional energy, and other resources on individuals who do not meet their mating needs. For example, women are more distressed by a partner's deception based on status, resources, and the depth of emotion prior to sex and men are more distressed if deception relates to the likelihood of sexual activity (Haselton et al., 2005). Further, single women, who

may wish to form a new relationship, are better than women who are in committed relationships, at detecting men "faking good", i.e., those who use enhanced descriptions of themselves in a manner that might appeal to potential partners (Johnson et al., 2004).

Deception Relating to Sexual History

Positive self-presentation is essential for those wishing to attract and retain a romantic partner. Full disclosure of a person's sexual history may lower their attractiveness if that sexual history is perceived to be inappropriate or excessive. Indeed, the ramifications of an undesirable sexual history may extend beyond the potential or current partner to a "bad" reputation and wider social stigma. Girls and women are particularly susceptible to such societal judgment and are more likely to be criticized or bullied by their peers than boys and men who engage in the same sexual behavior (Dunn et al., 2017). Indeed, such information may be used against romantic rivals when competing for potential mates (Reynolds et al., 2018). Reflecting these concerns, many people avoid disclosing their sexual history. For example, Stebleton and Rothenberger (1993) report that all men participating in their research had failed to disclose their sexual history to at least one partner.

Sexual history-based deception may extend beyond basic partner number. For example, people may conceal or falsify the identity of their previous partners or the prior incidence of infidelity (Williams, 2001). Those who have been unfaithful in previous relationships are more likely to be unfaithful in their current relationship (Adamopoulou, 2013). Hence, concealing prior infidelity may reduce the suspicion of the current partner, lower relationship conflict, and reduce the tendency for the partner to monitor behavior for signs of infidelity. Those who avoid the subject of previous romantic and sexual relationships may experience less emotional closeness and intimacy with their current partner. Indeed, people are less likely to trust those who fail to self-disclose and share significant personal information (Willems et al., 2020). As a consequence, men and women who do not wish to reveal their sexual history may choose to actively deceive rather than engage in deception by omission (i.e., avoid the subject). According to Horan (2016), approximately 60 percent of those questioned had actively misrepresented their sexual history (i.e., number of previous sexual partners). Further, approximately half of those questioned plan to lower the number of previous partners disclosed to future relationship partners (Cochran & Mays, 1990).

Sexual history-based deception can also have a significant impact on the

long-term health and well-being of the deceived partner. For example, Desiderato and Crawford (1995) report that 42 percent of those who had currently or previously had a sexually transmitted disease did not tell partners before sexual involvement and 17 percent of those who were diagnosed as HIV positive did not inform partners about their status. As many sexually transmitted diseases result in compromised fertility (Brunham et al., 1991), sexual deception could have considerable long-term consequences for the deceived partner. Of course, a range of factors may impact on the perceived sexual history of an individual and presumed risk of unprotected sexual activity including physical attractiveness (Eleftheriou et al., 2016; Lennon & Kenny, 2013).

Online Dating

> "I have actually met a lot of people online. Most of the men seem much better online than they are in person. Most are married, and most lie."
>
> —Albright, 2007, p. 86

Researchers have often focused on face-to-face romantic courtship; this is not, however, the only way in which couples establish or maintain romantic relationships. In recent years, the use of online dating services, such as websites or apps, has become particularly popular and a wide range of dating sites are available (Madden & Lenhart, 2006; Sprecher et al., 2008). For example, these may be focused on the formation of casual or committed relationships or even extrapair relationships. Online dating sites may match individuals according to their profile or allow users to view profiles and decide themselves if they would like to connect with that person. Compared to traditional methods, online dating has many advantages. For example, it provides access to a large pool of potential mates (Albright, 2007) and may be especially attractive for those in cultures that discourage frequent intersexual contact (Toma, 2017).

The number of people engaged in online dating, ease of "matching" with others, and hence scale of intrasexual competition may increase the tendency to misrepresent the self and present a more favorable profile. Indeed, deception is often regarded as the greatest disadvantage of online dating (Madden & Lenhart, 2006). As stated by one online dater, "to make a long story short … found out he was married … and the name I had been calling him for 10 months was not his … the job he spoke so highly of did not exist … I was crushed … But he is not an exception—in the 5 years of being single … there are a ton of people who lie… they do not see real people on the other side of their monitor" (Albright, 2007, p. 87). In part, the tendency to deceive online may reflect the nature of the

online environment.

Traditionally, people receive information about potential partners both through the “expression given” (e.g., symbols available through verbal or written communication) and “expression given off” (e.g., clothing, bodily posture, and appearance) (Goffman, 1959). Compared to offline communication, online dating provides users with much greater control over the information they present. This is exacerbated by the relative isolation of the online dating environment that reduces opportunities to verify the authenticity of information presented by the potential partner through contact with their wider social network. In the absence of visual cues, or visual cues provided only through the managed availability of photographs, online dating enables deception about the most fundamental information such as age, appearance, marital status, and even gender (Cornwell & Lundgren, 2001). Further, asynchronicity allows online daters to research and carefully consider a response which can facilitate the posting of false information, such as allowing a person to demonstrate an expertise that they do not actually possess.

The individual compiling the profile has complete control of the information provided and the individual viewing the profile is completely dependent on this, providing substantial opportunities for deception. It is perhaps not surprising, then, that misrepresentation is common in online dating. This deception appears to mirror offline sex differences and the characteristics sought by the opposite sex. For example, while women are more likely to misrepresent their physical attractiveness (e.g., weight) when dating online, men are more likely to misrepresent their marital status, personal assets (e.g., income or education), and relationship goals (e.g., interest in a long-term relationship) (Hall et al., 2010; Schmitz et al., 2013). Indeed, physical appearance is so influential that men rate an online dating profile more positively when paired with an attractive photograph, even when they know that the photograph does not feature the owner of the online dating profile. Women do not display this bias, with evaluations of an online dating profile unaffected by the presence of an attractive photograph that is unrelated to the dating profile (Bak, 2010).

Although online daters may first match online, the relationship is expected to move offline at some stage. Those engaged in online dating typically move from messages via the online dating site, to personal email, then telephone, and finally face-to-face meeting (McKenna et al., 2002; Merkle & Richardson, 2000). Though substantial misrepresentation may increase a potential partner’s initial attractiveness, this deceit would be revealed upon face-to-face meeting. Therefore, those creating an online dating profile typically seek to maintain a balance between the accurate, authentic, and desirable ideal self (Ellison et al.,

2006). People may reconcile any difference between their actual self and presented self by suggesting that the presented self reflects a former or future self and not regard this as deceptive. For example, the presented self may reflect a younger, more attractive version of the self or one who has already completed their education.

While 80 percent of respondents misrepresent at least one physical attribute in their online profile, the level of exaggeration is typically small, for example, three quarters of an inch for height, approximately six months for age, and nine pounds for weight (Toma et al., 2008). These exaggerations reflect the partner preferences of their preferred mate. For example, men are more likely to enhance their height in online profiles, reflecting the female preference for tall partners. The self-rated accuracy of online dating profiles is correlated with observer ratings of profile accuracy suggesting that these inaccuracies are intentional rather than a function of self-deception (Toma et al., 2008). The overall tendency to exaggerate rather than completely misrepresent for fear of rejection on face-to-face meeting is further indicated by research demonstrating that people are less likely to exaggerate their personal qualities if they believe that they will interact with the person face-to-face rather than email in future (Guadagno et al., 2012). Of course, more fundamental deception does sometimes occur.

Relative to the *use* of deception by those dating online, there is a paucity of information addressing the *detection* of deception during online dating. However, preliminary research indicates that women are more likely than men to detect deception during email at earlier stages of online dating whereas men are more likely to detect deception during the first face-to-face meeting (Schmitz et al., 2013). Indeed, users appear alert to the possibility of online deception, with more than 80 percent of online daters surveyed believing that others misrepresent their physical appearance (Gibbs et al., 2006). The extent to which deception in online dating impacts on the subsequent formation of a relationship also remains unclear. In one study, Sharabi and Caughlin (2019) surveyed online daters before their first date with a prospective partner. They also analyzed their email communication through the online dating site for linguistic markers of deception. Perceptions of the partners' but not their own deception predicted the success of the first date, as measured by the expectation of future interaction and altered attraction to the individual following the meeting.

Deception in Established Relationships

Most people report that deception in a romantic relationship is morally unacceptable (Peterson, 1996). Despite this, deception is relatively common in

romantic relationships compared to other relationship types (DePaulo & Kashy, 1998) with the majority of those questioned reporting that they have lied to a romantic partner (Boon & McCloud, 2001; Knox et al., 1993). Research indicates that, on average, people deceive their romantic partners 0.7 times per day, though there is considerable individual variation (Guthrie & Kunkel, 2013). Demographic factors are also important. For example, men are more likely to report that they would use deceptive strategies within existing relationships than women (Blair et al., 2001) and women report greater deception by relationship partners than men (Quirk et al., 2014). A range of commonplace relationship behaviors may be subject to deception such as expressing love and commitment (Stafford & Canary, 1991). Indeed, deceptive affection represents one of the most important deception types and may involve either withholding genuine affection or signaling affection that does not exist (Horan & Booth-Butterfield, 2013).

Deception is not, of course, restricted to face-to-face interactions between couples. In recent years, researchers have placed greater emphasis on the use of online or mobile communication within established relationships. For example, sexting, defined as sending sexually explicit text messages, photographs, or videos to another person, is relatively common. However, similar to online dating, the person receiving the sext is dependent on the sender for the authenticity of the information provided (Delevi & Weisskirch, 2013). According to Drouin et al. (2014), 48 percent of active sexters report having deceived their partners during sexting, for example, by lying about what they are wearing or doing. Deception during sexting appears to be more prevalent among women than men and is often employed to improve the partner's experience.

Deception can serve a number of important functions (Buller & Burgoon, 1998) and may benefit the person who is lying or another individual such as the partner being lied to. For example, benevolent deception, performed for prosocial reasons, such as to protect the feelings of a partner, is not malicious (Watt, 2008) and may reduce social tension or the likelihood of conflict (Tosone, 2006). Indeed, O'Hair and Cody (1994) state that "deception is a message strategy much like other forms of communication in that it is purposeful, often goal directed, and frequently functions as a relational control device" (p. 181). It is, therefore, important to consider the motivation and consequences of deception in established romantic relationships. In a diary-based study, Guthrie and Kunkel (2003) identified a range of motivations for deception within romantic relationships including relationship maintenance, establishing relationship control, and negotiating tension. With regard to relational control, one participant stated, "I did this to make her feel bad and then comfort her out

of this to build myself up" (Guthrie & Kunkel, 2003, p. 150).

The type or duration of the romantic relationship may influence the motivation for the deception. For example, in married couples, deception is more likely to reflect a concern for the partner whereas in dating couples, deception is more closely associated with a desire to continue the relationship. Further, individual differences are apparent (Cole, 2001). Women appear to tell more altruistic lies than men (DePaulo & Bell, 1996), and this tendency is present at a young age (Saarni, 1984). Of course, it may be difficult to differentiate these motives, either because the deception serves more than one function or because the person explaining their deception is unwilling to acknowledge or report their motivation for the lie.

When suspicious that their partner has been deceitful, people may choose to ignore the potential deception, search for additional evidence, discuss the situation with their partner, or terminate the relationship. A range of factors, such as individual differences and relationship quality, may influence this response. For example, those who are securely attached are more likely to discuss the deception with their partner while those with an avoidant attachment style are more likely to avoid their partner and are more willing to terminate a relationship following a partner's deception (Jang, 2008; Jang et al., 2002). Research indicates that termination of the relationship is not a common response to deception. Approximately one quarter of those questioned terminate their relationship (McCornack & Levine, 1990; Planalp & Honeycutt, 1985), though this is likely influenced by factors such as the type of deception involved and the length or seriousness of the relationship.

Even if the relationship continues, the deception may have important consequences for the couple and relationship outcomes. For example, deception threatens relationship trust (Bok, 1999) and increases uncertainty in a relationship (Planalp & Honeycutt, 1985). Hence, believing a partner to be dishonest is related to low levels of relationship satisfaction and commitment (Cole, 2001). Of course, though deception may have a negative impact on the romantic relationship, it is important to note that complete honesty may also lead to conflict and threaten the stability of the relationship. It is, therefore, important to consider both the potential harm associated with deception and the potential harm that may result from telling the truth. The decision to risk the negative consequences of deception may reflect both negative consequences of telling the truth and the tendency for people to believe that they are successful at deceiving their partner and hence can avoid the consequences of detection (Boon & McLeod, 2001).

Pretending Orgasm

> "Women might be able to fake orgasms, but men can fake a whole relationship."
>
> —Sharon Stone

A substantial body of research has focused on deception during sexual activity (e.g., pretending to orgasm). Research indicates that 75–90 percent of women do not consistently orgasm during sexual activity (Bancroft et al., 2003) and a substantial minority do not experience orgasm at all (Lloyd, 2005). Further, when women do experience orgasm it is most likely to be during oral sex or masturbation than penetrative sex (Brewer & Hendrie, 2011). Compared to the low incidence of female orgasm during sexual intercourse, pretending orgasm is relatively common among women. Indeed, research indicates that women use a range of cues such as breathing rate, body movements, and vocalizations to falsely indicate that orgasm has occurred. Brewer and Hendrie (2011) report that 56 percent of women vocalize, for example moan or scream, when they are not going to orgasm over 70 percent of the time, and 70 percent of women do so more than 50 percent of the time.

In Western contexts, men place considerable importance on their partner's orgasm (McKibbin et al., 2010), and the focus on female orgasm may encourage women to pretend. Women whose partners ask if they have experienced orgasm are more likely to pretend orgasm, and more than 50 percent of those who pretend report that they "feel guilty, but it is important to satisfy my partner" (Darling & Davdon, 1986). Detection rates appear to be low. Women report pretending orgasm more frequently than men perceive them to pretend (Thornhill et al., 1995) and only 55 percent of men believe that they can detect when their partner is pretending to experience orgasm (Mialon, 2012). Though pretending orgasm is often successful, i.e., it is undetected, the consequences when partners become aware of the deception are substantial. Indeed, reactions to a partner's pretending to orgasm are similar to responses to infidelity (Shackelford, LeBlanc, & Drass, 2000).

Motivation for Pretending Orgasm

Similar to other forms of deception, there may be a benevolent aspect to pretending orgasm. For example, 70 percent of women report pretending in order to avoid partner distress (Muehlenhard & Shippee, 2010) whereas 87 percent use vocalizations to boost their partner's self-esteem (Brewer & Hendrie, 2011). Hence, pretending orgasm signals sexual and relationship satisfaction and may serve to strengthen the relationship. To some extent, this may be an effective

strategy; men whose partners *appear* to frequently orgasm report higher relationship satisfaction (Kaighobadi et al., 2012). Women may also pretend to experience orgasm to reduce the likelihood that their partner will be unfaithful or end the relationship (Muehlenhard & Shippee, 2010). Indeed, those who pretend to experience orgasm in order to improve their partner's sexual experience are also more likely to engage in mate retention behavior including direct mate guarding such as keeping the partner under surveillance; positive inducements such as providing gifts, favors, or inducements; and public signals of possession such as bragging about their partner to other women (McCoy et al., 2014).

Individual Differences

Similar to other forms of deception, there is considerable variation in the use of pretending orgasm with both individual and relationship factors influencing engagement in this behavior. Single women are more likely to pretend orgasm than married women (Darling & Davdon, 1986), and pretending orgasm is more likely among lesbian and bisexual women than heterosexual women (Cooper et al., 2010). Research indicates that women with higher levels of sexual socialization involving behavior such as exposing one's body to gain sexual attention, those believing that sex can be a source of power, and women with higher sexual self-esteem, such as the tendency to evaluate oneself positively as a sexual partner, are more likely to pretend orgasm (Erchull & Liss, 2014; Wiederman, 1997). Hence, pretending to experience orgasm appears to be associated with power and control. Indeed, women with higher levels of Machiavellianism, characterized by a willingness to exploit others and a manipulative interpersonal style, are more likely to pretend orgasm in order to deceive and manipulate a partner (Brewer et al., 2016).

Women partnered to less agreeable or tolerant men, (Ellsworth & Bailey, 2013), women with a greater number of lifetime sexual partners (Wiederman, 1997), and those who have been or are likely to be unfaithful (Ellsworth & Bailey, 2013) are more likely to pretend orgasm, perhaps to reassure partners that they are satisfied with the relationship. This may serve to enhance or strengthen the relationship. The reassurance may also increase her partner's confidence in the relationship and reduce his monitoring of her behavior or mate guarding, which may afford additional opportunities for extrapair relationships. Women's attitudes toward sexual behavior and romantic relationships may influence the tendency to pretend orgasm or the specific motivations for doing so. Those engaging in sexual behavior to attain a goal, for emotional or physical reasons, or for reasons associated with insecurity are most likely to pretend

orgasm (McCoy et al., 2014).

Men Pretending Orgasm

Women are more likely to pretend to experience orgasm during sexual intercourse than men (Thornhill et al., 1995). However, 25 percent of heterosexual men report having pretended to experience orgasm on at least one occasion (Muehlenhard & Shippee, 2010). The deception may involve verbal signals, such as stating that they are about to orgasm or body movements, such as increasing the speed or strength of thrusting. Men appear more likely to alter their body movements than women when pretending orgasm (Muehlenhard & Shippee, 2010), though—compared to women's pretending—relatively few studies have addressed the incidence of men pretending orgasm.

Motivations for pretending orgasm include—similar to women—wishing to protect the feelings of their partner and to bring sexual intercourse to an end. Men also report pretending orgasm when they have experienced orgasm earlier the same day, when intoxicated, or when they do not wish their partner to know that they have not experienced orgasm, an event that is routinely expected of men (Muehlenhard & Shippee, 2010; Zilbergeld, 1999). As reported by one man, "One night after a couple hours of heavy drinking I was talking to this girl on my floor and apparently I was hitting on her. One thing led to another and I started sobering up during sex so I faked to make her go away. … She is unattractive/annoying [and I] wanted to get her off me … when my senses came about and I took my drunk goggles off" (Muehlenhard & Shippee, 2010, p. 558).

Infidelity

> "Someone told me the delightful story of the crusader who put a chastity belt on his wife and gave the key to his best friend for safekeeping, in case of his death. He had ridden only a few miles away when his friend, riding hard, caught up with him, saying 'you gave me the wrong key!' "
>
> —Anais Nin cited in Borden 2007 p96

Long-term romantic relationships are typically formed with the expectation of romantic and sexual exclusivity. Research indicates, however, that infidelity is widespread (e.g., Negash et al., 2014) and is most likely to occur when the primary relationship does not meet important needs such as intimacy, companionship, or sex (Lewandowski & Ackerman, 2003). In one study, 23 percent of men and 19 percent of women reported that they had "cheated"—engaged in sexual interactions with someone other than their partner, which could jeopardize, or hurt, their relationship—during their current relationship

(Mark et al., 2011). Infidelity is associated with a range of negative consequences including conflict, distress, and relationship dissolution and can impact on physical and mental well-being (Fincham & May, 2017; Shrout & Weigel, 2018). Unsurprisingly, then, given the widespread nature of infidelity and the potential consequences of such behavior, men and women are sensitive to the threat of infidelity.

Jealousy, though often conceptualized as a "dark" emotion, serves an important adaptive function. It is experienced in response to a real or imagined threat to the relationship and prompts men and women to respond to the threat. For example, mate-retention behaviors may be used to deter rivals or strengthen the relationship. Men and women do not necessarily differ with regard to the frequency or intensity of jealousy. Men and women do differ, however, with regard to the threats that elicit jealous behavior, which reflect the specific evolutionary pressures experienced by each sex. Female sexual infidelity places their male partner at risk of cuckoldry—unknowingly raising another man's child—with a substantial negative impact on his time, resources, and, if discovered, social status. Women whose partners are unfaithful do not face the risk of cuckoldry. The greater threat posed for women is the dissolution of the romantic relationship and loss of resources to another woman. Hence, although both sexes respond jealously to sexual (e.g., sexual intercourse with another person) and emotional (e.g., sharing personal feelings with another person) infidelity, sexual and emotional infidelity are associated with greater evolutionary consequences for men and women, respectively.

Research indicates that men experience greater distress to sexual compared to emotional infidelity and women display the opposite pattern (Buss, 2018). Research in this area has been criticized on both methodological and theoretical grounds. In particular, the use of forced-choice scenarios, in which men and women are asked to imagine that their partner has been sexually but not emotionally unfaithful or emotionally but not sexually unfaithful, requires participants to identify the most distressing scenario. Critics argue that though instructed to focus on one type of infidelity only, men infer that women would not engage in sexual infidelity without emotional infidelity and women believe that men would not engage in emotional infidelity without sexual infidelity. Despite these criticisms, sex differences in response to emotional and sexual infidelity have been routinely observed using a range of methodological techniques. These include the use of continuous response scales requiring participants to rate their distress to each scenario on a 1–7 scale (Bendixen et al., 2015). Overall, such sex differences appear robust to the theoretical and methodological approach of the researcher (e.g., Edlund et al. 2018).

Sex differences have also been identified in response to actual emotional and sexual infidelity. For example, when faced with their partner's infidelity, men are more likely to ask their partner about sexual aspects of the relationship whereas women are more likely to focus on emotional elements of the relationship (Kuhle et al., 2009). Further, Walsh et al. (2019) report that men are more likely to terminate a relationship in response to sexual infidelity and women are more likely to leave their partner in response to emotional infidelity. When confronted by a partner about their own infidelity, men are more likely to deny an emotional relationship and women are more likely to deny a sexual relationship (Kuhle et al., 2009).

Conclusion

Though men and women often emphasize the importance of honesty in romantic relationships, the use of deception is widespread. Deception may be employed in order to attract a partner or obtain sex. Deception is also common within established relationships and sexual activity itself. A range of individual and relationship factors influence the tendency to deceive, type of deception employed, and motivations for deceptive behavior. Deception in human mating is also influenced by the sex of the deceiver and the deceived. For example, men and women appear to employ different forms of deception; appealing to the type of partner and relationship most desirable to their potential mate. Caution is of course recommended when interpreting research findings which typically rely on the use of self-report data and is therefore reliant on deceivers being honest about their use of deception.

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CHAPTER 22

Marriage and Monogamy in Cross-Cultural Perspective

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Abstract

Much of our understanding of human partnership dynamics has historically come from a small subset of Western, industrialized societies, which share norms about monogamy and fidelity. Cross-culturally, however, there is substantial variation in both formal marriage systems and the role of nonmarital partnerships. Understanding this variability has important repercussions for evolutionary questions about mating and parenting, which this chapter addresses. In particular, the chapter covers (1) the evolution of monogamy; (2) variation in marriage and mating systems cross-culturally; (3) differences between social and genetic monogamy, and their repercussions for thinking about parenting and partnerships; (4) why concurrent and sequential partnerships might be adaptive, particularly in certain contexts; and (5) why the traditional relationship between paternity and paternal care is not always applicable. Throughout, I focus on data from non-WEIRD (non-Western, educated, industrialized, rich, and democratic) societies, as a counterpoint to the vast body of existing literature in psychology. Doing so allows me to highlight areas where universal patterns emerge and where cross-cultural differences are critical to understanding variation.

Key Words: marriage, monogamy, multiple mating, cuckoldry, divorce

Monogamy in the Animal Kingdom

Monogamy is a rarity in the animal kingdom. It is most common among

birds, occurring in somewhere around 90 percent of species (Cockburn, 2006), but it also occurs in some species of mammals, fish, and reptiles. Although it only affects a small subset of species, scientists continue to have rich and vibrant debate about how and why monogamy evolved. Explanations have included roles for infanticide prevention (van Schaik & Dunbar, 1990), the spatial distribution of females (Komers & Brotherton, 1997), mate guarding (Brotherton & Komers, 2003), and female choice (Gavrilets, 2012). But probably the most well-known explanation was that monogamy was driven by the presence of paternal care. The relationship between paternal care and monogamous mating continues to be an important facet of these debates, but newer models posit that monogamy likely predated paternal care, so the causal arrow has now flipped to show fathering behaviors as a response to rather than a cause of monogamous mating (Lukas & Clutton-Brock, 2012).

Despite the fact that paternal care is unlikely to be the original driver of pair-bonds, definitions of monogamy often include the notion that all offspring born to the pair will be fathered by its male counterpart. However, a pair-bond is no guarantee of sexual fidelity, and the rate of extra-pair paternity (EPP) varies widely across species (Cohas & Allainé, 2009; Griffith et al., 2002). For clarity, biologists introduced the terms “social monogamy” and “genetic monogamy” to distinguish between normative partnership practices and actual relatedness between members of the pair and their offspring. Social monogamy is typically defined as a pairing for the purpose of reproduction, often, but not always, co-occurring with biparental care. Genetic monogamy, on the other hand, requires an exclusive sexual relationship and is classified solely on the rate of EPP.

Birds provide the clearest example of this distinction. Social monogamy is more common among birds than any other class of vertebrates, and due to the high incidence of biparental care, it was long believed that genetic monogamy in birds was similarly widespread. But the advent of DNA fingerprinting turned this belief on its head. In one large multispecies study, true genetic monogamy (0 percent EPP) was found in only 14 percent of socially monogamous species with 90 percent of species exhibiting at least some EPP (Griffith et al., 2002). In addition, in some cases males titrated their care in accordance with paternity certainty (Møller & Cuervo, 2000), but in others high rates of EPP co-occurred with significant male care (Dixon et al., 1994). In unpacking this conundrum, Wright (1998) notes that understanding the relationship between paternity and paternal care requires a deeper understanding of a species’ life history, including assessing the costs and benefits of both providing care and seeking extra-pair mates.

Among mammals, social monogamy is much less common, but pair-bonded

species generally exhibit lower rates of extra-pair paternity than those seen in birds (Clutton-Brock & Isvaran, 2006). This leads to greater concordance between social and genetic monogamy. There are exceptions, however. North American beavers, who live in socially monogamous family units, were shown to have multiple paternities in more than half of all litters (Crawford et al., 2008). Tree shrews, who are closely related to primates, have also shown EPP rates at 50 percent (Munshi-South, 2007).

When we look even closer to home, among our primate relatives, the relationships among monogamy, fidelity, and paternal care are even more complex (Fuentes, 1998). Social monogamy is more common in primates than among mammals in general, occurring in about 29 percent of species, but is still in the minority (Lukas & Clutton-Brock, 2012). Genetic paternity studies among monogamous primates show a range in EPP, with several species exhibiting true genetic monogamy like the Azara's owl monkey (Huck et al., 2014), while others like the fat-tailed dwarf lemur have EPP rates as high as 47 percent (Fietz et al., 2000). Some pair-bonded species share important similarities with humans, including biparental care and cooperative breeding, forming a structure much like a nuclear family. But complicating things further, monogamy is not required for paternal care. Mountain gorillas in both single-male and multimale groups exhibit parental care, which is linked to increased fitness for males (Rosenbaum et al., 2011; Rosenbaum et al., 2018). Given that humans practice a variety of mating systems, including monogamy, polygyny, and polyandry, the behavior of mountain gorillas may be as useful as that of monogamous gibbons for thinking about parenting and partnerships in humans.

What makes humans distinct is that the variation we see in other species, in humans is magnified by culture. For example, two recent reviews of monogamy in mammals found that a key predictor of the level of EPP was whether bonded pairs live alone or in a group setting, with group-living species exhibiting higher rates of EPP (Cohas & Allainé, 2009; Lambert et al., 2018). Humans of course also live in groups, made up of bonded family units, so from that we might expect humans to have relatively high levels of EPP. But while living in groups can open up opportunities for extra-pair partnerships, it can also lead to stringent cultural norms promoting monogamy and increased opportunities for monitoring and punishing norm violators. Other ecological and demographic predictors that have proven useful in cross-species analyses, like the adult sex ratio and the distribution of resources, similarly become more complicated to analyze in humans because they occur within specific cultural milieus. This is not to say that ecological and demographic factors are unimportant in humans, just that they must be viewed in context. In viewing the various manifestations of

monogamy in the animal kingdom we can begin to see the breadth of what is possible, but culture makes the possibilities infinitely greater.

The Evolution of Monogamy in Humans

What can we take from the study of monogamy in other species that might be relevant to understanding diversity in our own partnership patterns? Debates about the role of paternal care in the evolution of monogamy are particularly prominent in the human literature (Kaplan et al., 2000). The "provisioning model" focuses on the importance of biparental care and, in particular, the role that male provisioning plays in promoting offspring survival (Lancaster & Lancaster, 1983; Lovejoy, 1981). In this model, joint production by husbands and wives is an adaptive strategy that emphasizes complementary tasks and coordination, resulting in greater fitness gains than either partner could achieve if they remained single (Gurven et al., 2009). The need for this cooperative system rests on the particularities of the human life history. With slow growth and a diverse and challenging skill set to learn, children remain dependent on their parents for an extended period, placing a burden on mothers that they are unlikely to be able to meet on their own (Gurven & Walker, 2006; Kaplan et al., 2000). Nuclear families are one solution to this problem. Evidence supporting this theory includes studies of the sexual division of labor, which allows men and women to specialize in their subsistence practices and provide a balanced diet of protein, fats and carbohydrates (Gurven & Hill, 2009; Winking, 2006), as well as studies showing the flow of resource transfers within families (Hooper et al., 2015; Marlowe, 2003a; Wood & Marlowe, 2013).

A challenge to the provisioning hypothesis is that to kick off the shift from the promiscuous mating system that was likely among our hominoid ancestors to a monogamous one, males would have faced a free-rider problem. Being an investor in a sea of noninvestors raises the risk of lost paternity and caring for nonbiological offspring (Hawkes et al., 1995). As in other species where social monogamy appears to precede paternal care (Lukas & Clutton-Brock, 2012), newer models focused on humans contend that paternal care is unlikely to have been the initial driver of long-term bonds in humans (Gavrilets, 2012; Schacht & Bell, 2016). Other explanations that have addressed the evolution of monogamy, like the distribution of females, are unlikely to be as important in a group-living species like humans (Kappeler, 2014). Instead, emphasis has shifted toward another demographic factor, the adult sex ratio (ASR) (Kokko & Jennions, 2008). When males are scarce and females abundant, there is little incentive for males to remain faithful, as they can easily find other partners, thereby

increasing their reproductive success. But when females are scarce, it behooves men to try to hold onto the mate they have, assuming they can attract one. Mate guarding then becomes an important strategy, which can lead to monogamy (Fromhage et al., 2005). Schacht and Bell (2016) apply this idea to the evolution of monogamy in humans, finding that mate guarding may have played an important role in the shift from multiple mating to pair-bonding, particularly when the ASR is at parity or male-biased. This leads to a question of whether a male-biased sex ratio was likely during human evolution. Schacht and Bell contend that it was. Menopause, which results in shorter reproductive lifespans for women compared to men, is one major reason (Coxworth et al., 2015; Marlowe & Berbesque, 2012). However, small populations in particular would have been prone to fluctuation in the ASR (Kramer et al., 2017).

Regardless of whether paternal care was the initial trigger for social monogamy, it is an important factor in mating and marriage decisions. For women, the provisioning work that men do has consistently been cited as an important factor when choosing a marriage partner. In a range of partner preference studies from small-scale societies women have been shown to value economic productivity in a long-term partner (e.g., Gurven et al., 2009, among Tsimane hunter–horticulturalists; Koster, 2011, among Mayangna foragers; Marlowe, 2004, among Hadza hunter–gatherers; Pillsworth, 2008, among Shuar foragers; Scelza & Prall, 2018, among Himba pastoralists). Most of these studies also show that men value economic productivity in a wife, indicating that not just male provisioning but a complementary division of labor is important in a marriage.

Diversity in Human Marriage Systems

When classifying the human mating system, most of the data that we focus on look at the practice of marriage. Marriage is the formally recognized union of two or more people, which brings with it a set of culturally recognized rights and obligations (Leach, 1955). It is an institution that serves multiple functions: as a social contract binding and obligating two sets of kin, as a core economic unit that controls the production and distribution of resources, and as a reproductive union that legitimizes offspring and fosters cooperative childcare (Murdock, 1949). When construed broadly, marriage is found in almost every human society, and is often viewed as a human universal (Marlowe, 2000; Murdock, 1949). In later sections of this chapter I delve into the adequacy of using marriage patterns as a proxy for determining a mating system, but I begin here by outlining the diversity in marriage practices. This diversity distinguishes

humans from most other animals, who typically exhibit one species-typical mating system. Chimps are promiscuous, gibbons monogamous, and howler monkeys polygynous. But humans cannot be so easily categorized.

Three main types of marriage occur in humans: monogamous marriage (one husband and one wife), polygynous marriage (one man and multiple wives), and polyandrous marriage (one woman and multiple husbands). When looking at how these practices vary across cultures, two important, and interconnecting, points emerge: (1) polygyny has been allowed in the majority of human societies, and (2) monogamy is the most common type of union (Marlowe, 2000; Murdock, 1967; Schacht & Kramer, 2019). These two facts can co-occur because the sanctioning and the practice of polygyny are distinct. Whereas more than 70 percent of societies have been shown to allow for polygyny, in most only a small fraction of men have more than one wife, making the majority of unions monogamous. This pattern holds across modes of production, with low levels of polygyny most frequent across settings (fig. 22.1).

What affects the degree of polygyny in a society continues to be debated. Factors associated with more polygyny have included variation in male control of resources (Sellen & Hruschka, 2004), pathogen stress (Low, 1990), and a female-biased sex ratio (Ember, 1974; Pollet & Nettle, 2008). Monogamy has been proposed to be more common when male contribution to subsistence is high (Marlowe, 2003b) and is also more common in larger state societies (Henrich et al., 2012; Sanderson, 2001).

Polyandry is another possible derivation from monogamy, but it is much rarer. Classical polyandry, where one woman is married to multiple men and the couple have a formally recognized union and shared residence, occurs in only a handful of societies, most notably in the Tibetan plateau and the Marquesas. Polyandry typically occurs when resources, particularly land, are scarce and where dividing them between brothers puts men at a disadvantage (Levine, 1988). There are other cases, however, where a woman has multiple concurrent partners with whom sexual access is relatively restricted and economic obligations exist, and these have been labeled “nonclassical polyandry” (Starkweather & Hames, 2012). For example, in South America there are a number of societies that practice “partible paternity,” where more than one man is formally designated as a father to a particular child and has obligations to invest (Beckerman et al., 1998; Hill & Hurtado, 1996; Walker et al., 2010). Although this definition increases the number of societies that can be labeled polyandrous, the frequency of polyandry within a given society is typically quite low. In classical cases it ranges between 9 percent and 50 percent of all marriages (Haddix, 2001) and is even less common in nonclassical populations

(Starkweather & Hames, 2012). Therefore, polyandry, like polygyny, is accepted in certain societies, but monogamous marriage remains the most common practice.

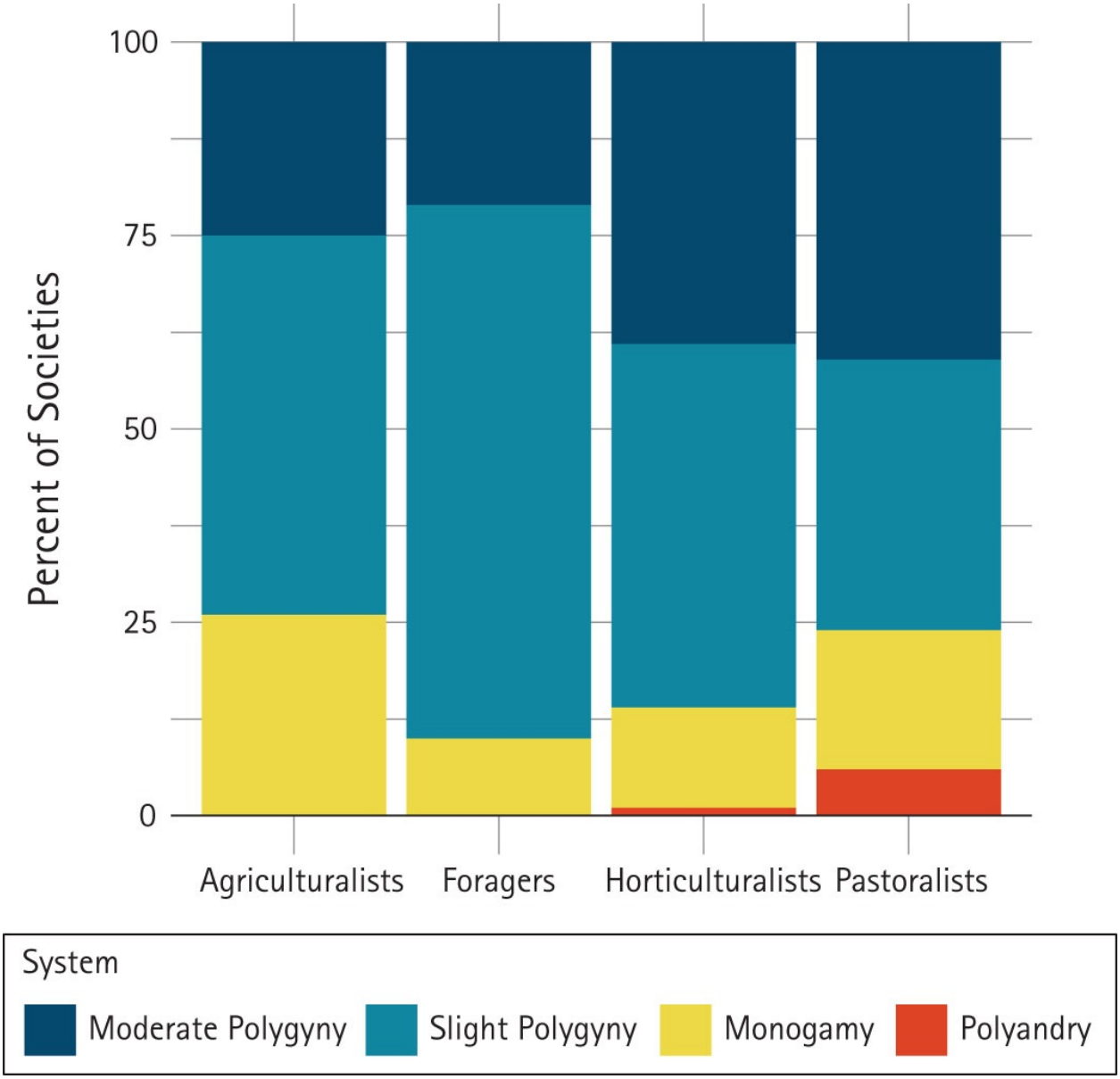

Figure 22.1 Cross-cultural marriage practices. Data are from the Standard Cross-Cultural Sample, as coded by Marlowe (2000).

What Makes Marriages Last, and What Makes Them End?

One other important feature of human marriage is its longevity. Long-term stability is a hallmark of marriage, and without it, the economic, social, and

reproductive functions of marriage are jeopardized. While the phrase “til death do us part” implies a lifelong commitment, divorce and remarriage are common across societies. In an analysis of 186 societies in the Standard Cross-Cultural Sample, Betzig (1989) found that only five reported divorce as rare or absent.

Divorce occurs for many reasons, but chief among them is infidelity (Shackelford, 1998). In addition, there is a clear double standard in how adultery affects divorce. Betzig reports fifty-four societies where divorce occurs only after adultery by the wife, compared to only two that follow from adultery only by the husband. Adultery by either spouse puts a marriage in jeopardy, but the ways in which it does so differ for men and women.

Betzig includes cowife conflict and elopement with a lover in her categorization of adultery. She does so because of the ways that marital systems affect extramarital sex. Cowife conflicts often erupt when men take on too many wives or pay more attention to one than the other. Because polyandry is much less common than polygyny, the opposite is rarely an issue. As Betzig writes, “when a married woman prefers a lover, she divorces her husband to marry him; when a married man prefers a lover, he may simply add her to his collection of wives” (Betzig 1989, p. 661). In societies where only monogamous marriage is condoned, that double standard should disappear, although patterns of remarriage still show strong sex differences, as we will see below.

While infidelity is a clear indicator of divorce (more about this below) there are other population-level indicators of marital stability that have been identified through cross-cultural work. The level of interdependence between spouses has been shown to be particularly important. In societies where women have few alternative sources of support (allomothers), divorce rates were lower (Quinlan & Quinlan, 2007). The same study shows an interesting quadratic effect of male provisioning. Where male contribution to subsistence was low, divorce was common, but it became more common again when male contributions were very high, making marital stability most likely when men and women contributed equally, supporting models of a complementary division of labor.

Another factor that has been shown to affect marital stability across groups is the ratio of males to females in the population. Traditionally, sexual selection models posited that an abundance of males would lead to greater male–male competition and more focus on mating effort over parenting effort (Emlen & Oring, 1977; Trivers, 1972). This would lead to the prediction that marital stability would be greater when females are in abundance. But newer models propose the opposite, that when the sex ratio is male-biased, men face steeper costs to desertion as there are fewer women available to partner with (Kokko & Jennions, 2008; Schacht et al., 2014). Therefore, a male-biased sex ratio is

predicted to be associated with greater partnership stability (Pollet & Nettle, 2008). Cross-cultural demographic evidence has largely supported the newer models. Blurton Jones and colleagues show that the primary predictor of marriage stability among four hunter–gatherer groups (Hadza, Ache, Hiwi, and !Kung) is “fertility units per male” a measure similar to the operational sex ratio (Blurton Jones et al., 2000). Where there are more women available, divorce rates are higher. In the United States, men were found to be more likely to be married in areas where there were fewer women (Schacht & Kramer, 2016), in the Caribbean fewer women were associated with greater marital stability (Otterbein, 1965), and in Denmark divorce rates were higher when there were more members of the opposite sex in the same occupational sector, where occupation was used as a proxy for the local mating market (Uggla & Andersson, 2018). Finally, as an indication of how quickly ASR changes can affect marriage practice, in Columbia, where excess male mortality has risen, leading to a female-biased sex ratio, marriage rates have dropped (Jones & Ferguson, 2006).

When Is Monogamy Monogamous?

As shown, fidelity is an important factor in predicting the stability of marriage, and this brings us back to the distinction between social and genetic monogamy. While fidelity is widely viewed as a core tenet of marriage, extramarital sex is common across cultures (fig. 22.2). Across 185 cultures, 39 percent are reported to be accepting of extramarital sex (Ford & Beach, 1951) and another cross-cultural study showed that it was rare or absent for men in only 20 percent of societies, and for women 27 percent (Broude & Greene, 1976). There is also often a double standard; restrictions against extramarital sex are routinely more rigid for women than men (Broude, 1980). But even for women, extramarital sex occurs at moderate to universal rates in 57.1 percent of societies in the Standard Cross-Cultural Sample (Broude & Greene, 1976). While it occurs across modes of production, female multiple mating is most frequent in horticulturalist societies and least frequent among intensive agriculturalists (Scelza, 2013).

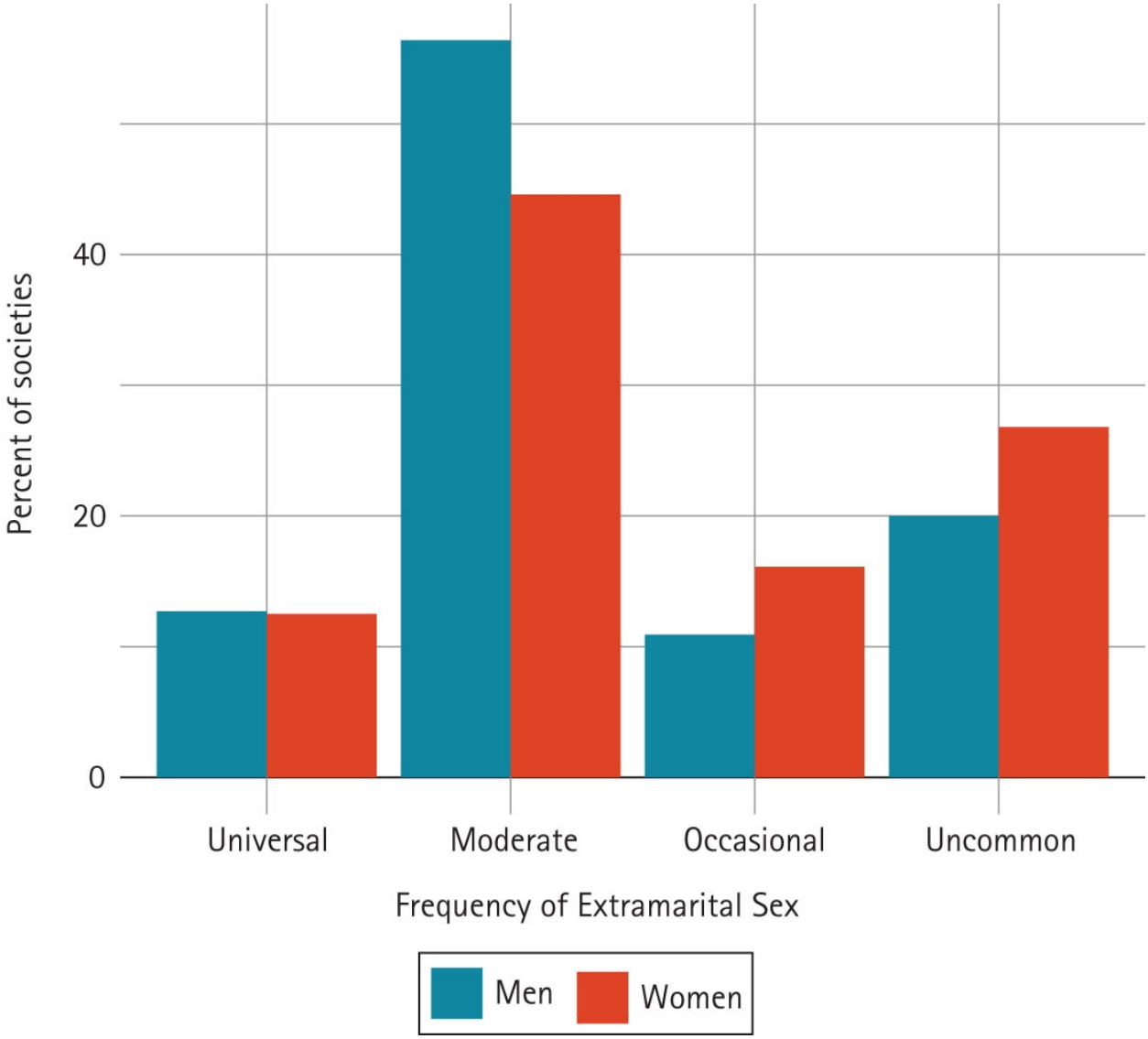

Figure 22.2 Cross-cultural variation in the frequency of extra-marital sex for men and women. Data are from the Standard Cross-Cultural Sample, as coded by Broude and Greene (1976).

Although it occurs commonly, there is tremendous variation in how extramarital sex is treated. In many places, including most industrialized countries that have adopted Christian mores and values, extramarital sex is strongly sanctioned. But in other cultures there are rules and norms that govern extramarital sexual activity, and often these rules protect women's sexual autonomy. In some places, certain categories of extramarital sex are normatively sanctioned, such as sex with particular kin or clansmen of the husband (Beckerman, 2005; Broude & Greene, 1976). Among the Oromo of Ethiopia, women would have sex with the friends and relatives of her husband. The husband would place his spear outside the home of the woman, and "Should the

husband return and find the spear, he should go back. Failure to do so would be considered as the violation of woman's rights," (Kelbessa, 2017). Similarly, in Zimbabwe, it is reported that men should alert their wives of their approach if they return home unexpectedly, in order to ensure he does not catch her with her lover (Arnfred, 2004). In my own conversations with Himba pastoralists, men describe a similar rule, that if a husband is out after dark he should find somewhere else to sleep that night, so that he does not come home to find his wife with her lover.

Evolutionary anthropologists have theorized about when and why extramarital sex occurs, both within and between societies. Just as they are linked to greater marital instability, female-biased adult sex ratios have also been associated with more concurrent partnerships (Jones & Ferguson, 2006) and a greater propensity toward infidelity (Arnocky et al., 2016). In Guyana, Schacht and Borgerhoff Mulder (2015) looked at sex ratio variation across ten populations and found that where the ASR is female-biased, men are more oriented toward short-term mating. There is also intrapopulation variation that is important to consider. In a study of Tsimane, Winking and colleagues show that the timing of extramarital affairs is related to where a man was in his reproductive career. Extramarital affairs were concentrated early in marriage, and declined as his number of dependent children rose (Winking et al., 2007). This supports the provisioning model of marriage mentioned earlier, as men appear to put more energy toward mating. Also in the Tsimane, it was shown that higher status men had more extramarital affairs (Von Rueden et al., 2010). Less is known about what predicts variation in women's engagement with extramarital sex, though one recent study showed that women who reported greater resource stress were more open to potential extramarital partners (Prall & Scelza, 2020a).

Of particular consequence to evolutionary scholars is how often extra-pair sex leads to extra-pair paternity. It is possible that while extramarital partnerships are common, they are unlikely to result in EPP. If coitus during extramarital partnerships is infrequent, the chance of conception for any partnership could be low, even where the partnerships themselves are normative. A discrepancy could also occur if it is only married men having affairs, as is the case in places that have the double standard for infidelity mentioned above. If married men father children with unmarried women, their babies would be categorized as nonmarital rather than extramarital births, as births are categorized by the mother's marital status rather than the father's. Finally, contraception, either through natural or medical means, could disrupt the relationship between extramarital sex and extramarital reproduction (Goetz et al.,

2019).

Current genetic evidence largely supports a notion of low EPP. In a summary of contemporary and historical genetic studies, it was found that across time, levels of EPP were stable at around 1 percent (Larmuseau et al., 2016). In another cross-cultural study, Anderson put the average rate at 1.9 percent (Anderson, 2006). Evolutionary psychologists, who lean more heavily on Western studies of infidelity for cues, speculate that slightly higher numbers may be normative, at around 10 percent (Baker & Bellis, 1994; Platek & Shackelford, 2006). However, a significant limitation of both the genetic and evolutionary psychology literatures is that they are heavily reliant on samples from American and European populations. These are cultures with long histories of strictly enforced monogamy, strong norms stigmatizing individuals (particularly women) who commit adultery, and religious and legal institutions that canonize fidelity as a core component of marriage. They are therefore exactly the populations where we would expect to find a low rate of EPP. But if we want to understand the true diversity in EPP across human populations we need genetic data from a range of populations, which mirror the variation we see in rates of extramarital sex.

These data are beginning to emerge, but genetic paternity studies raise a host of ethical issues, which can render such research impossible in many locations (Scelza et al., 2020a). Asking about infidelity is often inappropriate, and paternity even more so. Places where these data are more attainable tend to lie at the opposite end of the spectrum from the European and American studies, places where concurrent partnerships are frequent and normative and are not heavily stigmatized. One such study, among Himba pastoralists living in northwest Namibia, showed an extra-pair paternity rate of 48 percent, with more than 70 percent of married couples having at least one child fathered by someone other than the husband (Scelza et al., 2020b). Anderson (2006) describes a range of studies where limited information is known, but where the EPP ranges from 2 percent to 32 percent. However, we know very little about the ethnographic context of the data constituting these studies. Although more studies are clearly needed, even this small sample demonstrates the potential variability in EPP across human populations. This raises subsequent questions about whether and when EPP might be adaptive. In the next two sections, I address this question more deeply, first from the perspective of women and then men.

The Value of Concurrency

Traditional sexual selection theory posits that males are much more likely

than females to benefit from having multiple sexual partners. In Bateman's classic paradigm, there is a linear effect of additional partners for males, while females show limited returns after the first partner. These curves rest on the relationship between mating success and reproductive success, a relationship known as the Bateman gradient (Arnold, 1994). However, a wave of both theoretical and empirical work from the last twenty years has overturned traditional thinking about the value of multiple mating for women (Jennions & Petrie, 2000; Kokko & Jennions, 2008; Kokko & Rankin, 2006). In one cross-cultural study, Brown et al. (2009) show that rather than a consistent sex difference in reproductive variance that might be predicted by Bateman, there is no universal pattern. As expected, in polygynous societies men tend to have more variance than women, but in monogamous groups variance was relatively similar. Other ethnographic cases flip sex role stereotypes completely, showing that in rare cases women can benefit more than men from having multiple partners (Borgerhoff Mulder, 2009).

These new models coincided, in large part, with an influx of women scientists, who challenged our thinking about sex roles, and began asking new and different questions (Fausto-Sterling et al., 1997; Gowaty, 1996; Hrdy, 2009). As evolutionary biologist Patricia Gowaty wrote in 1996, "one of our difficulties in understanding monogamy is our lack of data about females' lives, perpetuated through the lack of adequate theory focused on females" (p. 22). In response, there has now been increased attention to the ways in which women can (and do) benefit from having multiple partners, and several explanations for women's concurrency have now been posed, including dual-mating, trading-up, and multiple investors (table 22.1). Here I review these three main explanations. For a more exhaustive list, see Buss and Greiling (2000). Rather than viewing them as mutually exclusive and competing explanations, I look to the cross-cultural literature to understand when and why one pattern may be more prominent than another.

Table 22.1 Potential Benefits of Female Multiple Mating

Strategy Type	Benefits to Women	Evidence for Hypothesis	Evidence against Hypothesis
Dual mating	Women gain from having long-term partners who are stable, high investors and concurrent short-term partners with "good genes"	**Japan/Britain**: Penton-Voak et al. (1999) **US:** Larson et al., (2013); Pillsworth & Haselton (2006a)	**Poland:** Marcinkowska et al., (2018) **US/Germany**: Jünger et al., (2018) **Himba**: Scelza and Prall (2018)
Trading Up u	Women can utilize short-term relationships as a way to evaluate men's potential as long-term partners,	**US:** Greiling & Buss (2000) **Pimbwe**: Borgerhoff Mulder &	**Canela**: Crocker & Crocker (2004)

	especially in comparison with their current partner	Ross (2019) **Ache**: Hill & Hurtado (1996)	
Multiple Investors	Resources from multiple men can provide either supplementary or complementary support for women and their children.	**Ache:** Hill & Hurtado (1996) **Bari:** Beckerman et al. (1998) **Himba**: Scelza & Prall in prep **Inuit**: Guemple (1986)	

All three of these explanations for female concurrency rest on the same fundamental evolutionary principle: the limiting resource for males and females differs. Where females have higher obligate costs of parental care (e.g., pregnancy and lactation) they will be "off" the mating market for longer, creating an imbalance in the operational sex ratio (Emlen & Oring, 1977). This means that for men, women are the limiting resource. For women, who have greater obligate parental care, they are limited in the resources they need to provide for themselves and their children. These differences underlie "sexual strategies theory" ' (Buss & Schmitt, 1993). In particular, sexual strategies theory (SST) focuses on the temporal context of human mating, noting that both long- and short-term partnerships were likely to have been part of our legacy. According to SST, because men are limited by the number of women they have access to, they should generally favor short-term partnerships more than women, as a way to increase fitness. Women, on the other hand, who are resource-limited, should be interested in multiple mating when it can increase their access to basic needs and services. What new models of sexual selection critically add is that even though women are the limited sex, male–male competition does not necessarily lead to more mating effort and more promiscuous tendencies for men. In some cases it might be more logical for men to commit to the partner they have, because finding another one will be difficult (Kokko & Jennions, 2008). Men might also expend more energy on investment if female choice is focused on the quality or quantity of care a man provides (Alonzo, 2012; Hoelzer, 1989).

Building from SST, dual-mating theory (DMT) proposes that women will prefer different traits in long- and short-term partners. In an ideal world, women should prefer a partner who will be both a reliable long-term investor and of high genetic quality. However, the authors theorize that attractive men are in greater demand, so those men will expend more energy on mating effort, making them less desirable long-term mates (Pillsworth & Haselton, 2006b). Therefore, preferences for long-term partners should be based on their potential as fathers and providers, including traits like wealth, kindness, and stability. Short-term

partners, according to this theory, should be favored mainly for their genetic potential. A suite of studies investigating the role of "good genes," often using proxies of masculinity as a cue of good health and immunocompetence, have been conducted in WEIRD (Western, educated, industrialized, rich, and democratic) settings, showing consistent differences (for a review, see Gildersleeve et al., 2014). Outside this context, little work has been done. There have been a few studies of partner preferences in small-scale societies, but most have not directly tested DMT because they have focused on only long-term partnerships. One exception is a study of Himba, which looked at preferences for formal (marital) and informal (nonmarital) partners (Scelza & Prall, 2018). While DMT is explicitly about women's preferences, this study found that men had dual preferences, favoring attractive girlfriends and hard-working wives. Women, on the other hand, focused on resource-related traits for both boyfriends and husbands, but proxies for these differed based on partner type. Within marriage, husbands are obligated to share their wealth with their wives, which led to women preferring a straightforward wealth measure as their preferred trait. In boyfriends, however, giving is optional, and because this is the case, women placed generosity above wealth in their rankings.

One of the most prolific, and controversial areas of study based on DMT is the hypothesis that women's preferences will change across her menstrual cycle. DMT proposes that when women are in the high-fertility ovulatory phase of their cycle, they will prefer short-term partners exhibiting traits linked to "good genes," whereas at points of low fertility they will prefer long-term partners who display traits for prosciality and being a being a good father and provider (Gangestad & Haselton, 2015; Pillsworth & Haselton, 2006b). Although some studies have shown positive evidence that women shift their preferences toward short-term and/or more masculine partners, a number of methodological critiques have recently been raised about this body of work, including issue of sample size and a reliance on self-reported cycle data (Jones et al., 2019), and other studies have failed to replicate the original findings (see Stern & Penke, this volume).

Cross-cultural tests of cyclical shifts in preferences are very rare, in part because of methodological and logistical challenges. Women in non-WEIRD societies spend more of their reproductive careers either pregnant or lactating, with only small windows of fertility between pregnancies (Strassmann, 1997). This makes tracking days of high and low fertility more difficult, and compounds already challenging issues of sample size. In addition, ecological factors have been shown to affect women's preferences for masculinity, and these generalized effects could swamp intraindividual differences in women's

preferences for short- and long-term partners (though to my knowledge these two factors have not been considered together empirically).

There are several other reasons why DMT might fail to replicate outside the WEIRD context. First, Pillsworth and Haselton (2006b) argue that sexually attractive men will be in greater demand, making them poor long-term partners. Their logic follows from Trivers (1972), who focuses on the trade-off between mating and parenting. This is certainly one possibility, but other studies have shown that factors such as wealth and status are strong predictors of male reproductive success (RS) both within and outside marriage (Von Rueden et al., 2010; Von Rueden & Jaeggi, 2016) making the link between "good genes" and short-term mating less clear. Between societies, the importance of DMT might depend on how valuable genetic quality is to a woman, compared to other benefits an extra-pair partner could bring in. In a cross-nation study using World Health Organization (WHO) measures of health and mortality, DeBruine et al. (2010) showed that women were more likely to prefer masculine faces in places with poorer health indicators. Within populations, we might also expect that there is variation in who enacts a DMT strategy. Women with high value on the mating market may be able to attract partners with both good genes and resources and ensure fidelity, due to dynamics of assortative mating, making dual mating unnecessary for them. These speculations remain largely untested, however, particularly outside WEIRD societies.

A second explanation for women's concurrency links to the practice of serial monogamy. "Trading-up" (Halliday, 1983; Jennions & Petrie, 2000) is the practice of engaging in concurrency as a way to test out new partners without having to give up one's current mate. Think of it like an interim period of nonmonogamy bookended by two monogamous relationships. Trading-up can occur serially as well, but this would entail a period of being single, which if resources are scarce could be very costly. Those costs must be weighed against the costs of getting caught. More broadly, "mate-switching" encompasses trading-up along with other explanations for transitioning between partners, including keeping another partner as mate insurance and divesting in partners who inflict costs (Buss et al., 2017) Empirical evidence of mate switching is rare, but mostly because it is understudied rather than because it has been looked for and not seen. Greiling and Buss (2000), in a set of studies conducted in the United States, reported that women are more interested in extra-pair partners who are more desirable and compatible than their current partner. A study of marriage patterns among Pimbwe horticulturalists in Tanzania showed that women with more spouses had greater reproductive success, and the authors speculate that this may be due to women "trading up" in order to improve their

economic circumstances (Borgerhoff Mulder, 2009). This study did not look explicitly at periods of overlap, but they did note that extramarital affairs typically lead to divorce and remarriage (Borgerhoff Mulder & Ross, 2019).

A third reason why women might engage in concurrent partnerships is that it enables them to acquire resources independently from multiple partners. Having more investors can either increase the total amount of resources available to them, in supplementary or complementary form, or reduce stochasticity in resource access, reducing the chances of shortfall. The value of multiple mating as a resource acquisition strategy in humans has received pushback almost since its inception. As Don Symons wrote in 1982, "Why should a female be better off with ten males, each of which invests one tenth in her offspring, than with three males, each of which invests on third unit, or with one male, which invests one unit?" (Symons, 1982, p. 299). This viewpoint assumes that all men are equal partners, a proposition that is rarely true, and which we should expect to vary depending on the socioecological context. For example. among Bari, as in many societies that practice "partible paternity," women can name multiple men as fathers of their child, and those men have obligations to support the women during pregnancy and support the child after its birth (Beckerman et al., 1998). They further found that children with secondary fathers were significantly more likely to survive to age 15 than those with only a single named father. Beckerman surmises that the additional calories that secondary fathers were directing to their children reduced stochasticity in access to food, rather than just providing more calories.

Another example comes from studies of Inuit marriages, where there is a practice of exchanging marital partners, and this too has been linked to resource security, in this case benefiting both the husband and the wife. Guemple wrote (1986), "Common exchange was at that point viewed as a form of extra-domestic marriage that was ecologically adaptive, lending an added flexibility to the organization of domestic life by providing both marriage partners with one or more additional 'spouses' whose services could be called upon in the event of a crisis of some sort … it is well established that exchanging couples met on a fairly regular basis and exchanged services of all sorts" (p. 20). Himba pastoralists also face resource scarcity, as microclimates combined with recurring drought can affect some men's livestock more than others, even within the same general area. This likely leads to the preference rankings described above, where women prefer resource-related traits in both husbands and boyfriends (Scelza & Prall, 2018). In a follow-up study, we found that Himba women who have multiple partners report that while resource transfers from their husbands are more reliable, boyfriends provided an important source of

support. This translated into measurable outcomes, with women who had both marital and nonmarital partners having greater food security (Scelza, Prall & Starkweather 2021). Although these examples all come from contemporary populations, resource scarcity, or at least stochasticity, is likely to almost always have been a hallmark of food production for humans, indicating that this could be one of the primary reasons female multiple mating occurred across time.

These explanations are not mutually exclusive, either within or between societies. Studies that compare explanations for extra-pair partnerships in women find multiple explanations are viable (Greiling & Buss, 2000; Walker et al., 2010). Rather, it will be important in future work to think about how different strategies might be more or less important in a particular context, as well as how strategies will differ among individuals within the same community and within the same individual across her lifespan.

The Cuckoldry Conundrum

There is a widespread assumption within the evolutionary social sciences that men should be extremely wary of investing in offspring, unless they can be very certain of their paternity (Platek & Shackelford, 2006; Wilson & Daly, 1995). Because of this, the term “cuckoldry,” the unwitting investment by a male in another male’s offspring, is often used to describe nonpaternity events in humans (Geary, 2006). But are men really being tricked into investing in children who are not their own? To address this question we need to understand the costs, and possible benefits, of nonpaternity, and once again it is helpful to look broadly across societies.

Most existing work in humans on this topic comes from WEIRD societies where fidelity is highly valued, and misallocations of investment are very costly. They are also places where EPP tends to be very low. In this context, where the costs are high and there are few, if any, benefits, it is reasonable to believe that men should be vigilant about paternity and seek to titrate their investment based on their paternity confidence. But what do we make of contexts where EPP is high? It would be a mistake to assume that men in these places are just worse at paternity detection, or that women are wilier in their pursuits to fool their partners. Instead, if we look at ethnographies about cultures where extramarital sex and EPP are normative, we find that “cuckoldry” is an unsatisfactory descriptor. Instead, paternity and paternal care are reflective of local context in ways that are likely to be adaptive.

As described above, we know little about the variability in EPP across cultures, so we must use rates of extramarital sex as a proxy. In a few places,

high levels of female concurrency co-occur with very low paternal investment. This was the case in some matrilineal societies like the Mosuo/Na, who traditionally practiced “walking marriage” (Hua, 2001). In this case women had lovers who would visit their natal homes. A woman might have one or many, but any children born to her belonged to her matrilineage and were the responsibility of her family to raise and care for. In cases like this, there is no “cuckoldry” to explain. But there are other examples of cultures where extramarital sex is normative and unstigmatized, and occurs within marital structures that obligate men to care for the children born to their wives.

Himba men are the fathers of all children born to their wives, regardless of paternity. The rate of EPP here is high (48 percent), but since this is one case where we have both genetic paternity data and men’s paternity assertions, we know that men are very accurate at detecting paternity (Scelza et al., 2020b). Being accurate at distinguishing in-pair from extra-pair children, however, does not lead to major differences in investment. As shown through a series of vignettes about paternal care, Himba have strongly held beliefs that children should be treated equally, regardless of paternity. Evidence of actual paternal care shows a more complicated picture, but one that exemplifies the interrelatedness of social and biological fatherhood (Prall & Scelza, 2020b). Anthropometric data show that extra-pair daughters are more likely to be nutritionally stressed than their in-pair counterparts, but there is no effect for sons. In contrast, extra-pair sons are more likely to be fostered out, but there is no effect of fosterage for daughters. It is possible that this is due to the benefits that children bring in to the household. Himba girls tend to do more labor than boys, and their work is less substitutable by the other gender. This could explain why extra-pair girls are kept in the household, but they might also be given more work, explaining their nutritional stress. Boys, who offer less have a higher net investment cost to fathers, which might explain why they may be less tolerant of extra-pair sons and foster them out. Interestingly, other forms of paternal care which are more visible, like bride price payments and livestock loans, show no differences between in-pair and extra-pair children. Shirking one’s paternal duties in these realms might be particularly costly as mens’ reputations can be harmed by showing bias toward biological children.

The Himba case exemplifies some of the ways that we can reconstitute the balance of gains and losses of nonpaternity. The costs of investing in nonbiological offspring may be outweighed by material or social benefits that children bring. In addition to their productive labor, children can also help to cement alliances between families, establish social cache, and provide support in old age. For example, among the Igbo of Nigeria if a woman’s husband is

infertile, it would be admissible for her to take a lover, which would still allow her children to be considered part of her husband's lineage, an advantage for husband, wife, and child (Kelbessa, 2017). Among the Kpelle of West Africa, Bledsoe explains that in traditional areas the economic importance of children meant that when there was a paternity dispute both the husband and the lover often try to claim the disputed child, with the husband sometimes even refusing compensation from the lover (Bledsoe, 1980). However, Bledsoe also writes that in areas that are more market integrated, the costs of children are beginning to outweigh the benefits, and as a consequence men are beginning to be more reticent to claim paternity when it is disputed.

Writing about the Inuit, Guemple emphasizes the role of labor exchange in marital partnerships, and notes that extramarital partnerships can help to build interfamilial cooperative relationships. This leads to biological paternity being relatively unimportant. He writes, "But if the relationship is formulated on a basis other than sexuality, or if children are not an expression of the acting out of that relationship, it follows that it does not matter where the children come from, who begets them, or even who they 'belong to' " (Guemple, 1986, pp. 20–21).

In polyandrous groups, notions of paternity have been directly linked to the functioning of this particular marital structure. Writing about Nyimba families in Nepal, Levine (1980) explained that in this system, where fraternal polyandry is the norm, all husbands have equal rights and access to their wife. However, Nyimba believe that each child has only one genitor, who is designated by the mother, and when the designated husband accedes, social and genetic paternity coincide. Despite singular notions of paternity, Levine (1980) wrote, "Joint household fathers, irrespective of the identities of genitor and pater, are expected to show affection to all children born within the marriage, contribute to their maintenance, and take part in their upbringing" (p. 290). Interestingly though, when the estate of a polyandrous household is partitioned, biological paternity rises in importance. While very young children remain with their mother wherever she resides, older children move to the home of their presumed genitor. Levine notes that paternity also plays a role in how property is divided, and even in the timing of household partitions.

These examples show that the distinction between maternal certainty and paternal uncertainty does not always put men at a disadvantage. Where social fatherhood is the currency that is linked to status, nonbiological children can enhance fitness. And where households rely on children for labor or other support, more can be better, regardless of genetics. As Bledsoe (1980) wrote in her study of social fatherhood among the Kpelle, "Ambiguity is often deliberately maintained, in fact, because of the manipulative advantages it

confers in different social and economic situations" (p. 29). The use of ambiguity, be it turning a blind eye, knowing but not acknowledging paternity disputes, or choosing when to acknowledge nonpaternity, demonstrates the inadequacy of the term "cuckoldry" to describe men's knowledge of and responses to nonpaternity. It should also be noted, that this does not dismantle predictions by evolutionary psychologists that men will have adaptations for mate guarding and paternity detection, as well as adaptations for differential investment based on perceived paternity probability, or that women will have adaptations to conceal nonpaternity. Rather, I argue that we should view these adaptations within their particular cultural context. In some cases detection of nonpaternity leads to strong sanctions, promoting a patriarchal system of mate guarding, female claustration, and subsequently low rates of EPP. In other cases, the same mechanisms for paternity detection can lead to tolerance or even acceptance of EPP, as men and women flexibly use that knowledge to make decisions about parenting and partnerships.

Conclusion

In the previous sections, I laid out the evidence for variation in human partnership patterns. Although long-term, cooperative partnerships are nearly universal in humans (be they monogamous, polygynous, or polyandrous), those bonds occur within a complex web of sexual strategies. These strategies often include deviations from strict pair-bonding. Both fidelity and rates of extra-pair paternity are clearly facultative. This variation has been a theme in the nonhuman animal literature, and we have seen significant theoretical leaps in work on sexual selection in the last twenty years. We now must meet their call and move toward more nuanced and contextualized empirical work on human parenting and partnerships.

In addition to making a general argument for a cross-cultural perspective on the study of human mating, I have tried here to explain not just *how* human partnership patterns vary but also *why* they do. For women, there appear to be myriad motivations for taking multiple partners, but these share a root in their emphasis on securing resources for themselves and their children. If we limit our research to societies where resources are plentiful, and where men's and women's labor and productivity are relatively equal, we limit our ability to understand the role that resources play in women's reproductive decisions. Motivations for multiple mating are expected to vary depending on socioecological factors; therefore, we must look at a range of modes of production and social structures to understand when and why certain

explanations for concurrency are more prominent in a particular place. Furthermore, within societies, we should also expect that there will be individual differences in women's motivations to engage in concurrency, and their ability to do so, based on their position on the mating market, their own needs and resources, and where they are in their life history. Similarly, when we look at fatherhood, we can see that attention to paternity is a recurrent theme, but paternity loss does not always mean that investment is being misallocated, nor does extra-pair paternity necessarily constitute an overall detriment to fitness.

A cross-cultural perspective on marriage and monogamy will be critical to the next phase of evolutionary studies on human partnerships. The literature continues to be dominated by studies conducted in WEIRD societies, by researchers from WEIRD countries (Pollet & Saxton, 2019). Expanding from this base will require thinking about data in nontraditional ways. One underutilized resource is existing secondary data from single-country and cross-national surveys, which often ask questions about marriage, monogamy, and parental care (Sear, 2020). Another is to move beyond the current dichotomy in the data, which tends to sample from either university populations or small-scale societies, and focus on the many (majority) of people who don't fit into either of those categories (Barrett, 2020). As an anthropologist, I would also advocate for the addition of more ethnography to the cross-cultural studies that are being done. Both our research design and the interpretation of our results can be enhanced by qualitative data that help us to make sense of cultural practices that are different from our own. The use of evolutionary theory to guide our research has been and can continue to be a fundamental strength, but there is room to also include descriptive studies and bottom-up observational work that helps us to identify outliers we might not predict using theory alone (Gurven, 2020). If we can view the unique breadth in mating practices that humans engage in as a feature we should focus on, we will come away with a deeper understanding of our behavior.

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CHAPTER
23

Sperm Competition

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Abstract

Sperm competition is a form of intrasexual competition in which the sperm of two or more males concurrently occupy the reproductive tract of a single female and compete to fertilize an available ovum. As a nonmonogamous species, humans have been subject to selection pressures associated with sperm competition. Consequently, human males have evolved a variety of anatomical, physiological, and psychological adaptations to address associated adaptive problems. Some of these adaptations motivate avoidance of sperm competition by engaging in precopulatory intrasexual competition, which may limit the risk of exposure to sperm competition. Other adaptations promote engagement in sperm competition during copulation or postcopulation and function not by avoiding sperm competition but by increasing the likelihood of winning the competition and siring offspring. For example, men facing a perceived increase in risk of sperm competition are more likely to demonstrate an increased interest in sex with their long-term partner. We summarize previous research on adaptations to sperm competition in humans, and highlight several directions for future research.

Key Words: sperm competition, cuckoldry, semen displacement, ejaculate adjustment, forced in-pair copulation, sexual coercion, female-directed violence, cryptic female choice

Sperm competition occurs when the sperm of two or more males concurrently occupy the reproductive tract of a single female. The extent to which sperm competition occurs in sexually reproducing species varies, from virtually

nonexistent in truly sexually monogamous species to extraordinary in polygynandrous species. As a nonmonogamous species, humans are subject to the risks of sperm competition. Some theorists argue that sperm competition has not been greatly influential over the course of human evolutionary history, and as evidence they point to historically and contemporary low discrepant paternity or cuckoldry rates in humans of around 1 to 2 percent (Greeff & Erasmus, 2015; Larmuseau et al., 2017; Larmuseau et al., 2013). Recent evidence indicates such rates may be culturally variable, and much higher in some cultures. For instance, extra-pair paternity is nearly 50 percent among Himba pastoralists of Namibia in southwest Africa (Scelza et al., 2020). In some cases, these instances of extra-pair paternity may not qualify as cuckoldry, per se, as the men and women involved in such cases seem to be accurately aware of the mismatch (Scelza et al., 2020). Even outside of such explicit cases of extra-pair paternity, people estimate local cuckoldry rates to be upwards of 10 percent (Voracek et al., 2009). So, although there is some disagreement about a species-wide rate of cuckoldry or extra-pair paternity, it is undeniable that cuckoldry at least occasionally occurs in humans, today and for much of our recent evolutionary history. Consequently, the risk of sperm competition in humans is certainly greater than zero.

Compelling evidence for the influence of sperm competition in humans is also apparent in the suite of purported adaptations that reduce the costs associated with sperm competition (for men) or promote sperm competition (for women). Such adaptations manifest at many levels—including anatomical and physiological features as well as psychological motivations and behaviors—and can and do operate at every stage of the mating process.

Testes Size

One of the most consistently identified anatomical features associated with sperm competition risk is relative testes size, which is a ratio of combined testes mass to overall body mass. Across numerous nonmonogamous species, from butterflies (Gage, 1994) and fish (Stockley et al., 1997) to birds (Møller & Briskie, 1995), rodents (Ramm et al., 2005), and primates (Baker & Shackelford, 2018a, 2018b; Møller, 1988), interspecific differences in relative testes size correlate with interspecific differences in risk of sperm competition. Experimental evidence from *S. stercoraria* confirms that increases in testes size are consequent to increased sperm competition, such that increases in sperm competition cause subsequent increases in relative testes size (Hosken & Ward, 2001). Larger testes are an adaptation to increased risk of sperm competition given that larger testes produce larger ejaculates, which increases a male's

chances of successful fertilization of an egg under circumstances of sperm competition (Møller, 1989). Among primates, human males have a relative testes size that is between gorillas' comparatively small testes (associated with very low sperm competition) and chimpanzees' comparatively large testes (associated with very high sperm competition). This suggests that human males, with intermediately sized testes, are subject to sperm competition at a rate between the highly competitive chimpanzees and the virtually noncompetitive gorillas (Baker & Shackelford, 2018a).

Semen Displacement

In addition to testes size, penis morphology may function as an adaptation to sperm competition. For example, the presence of penile spines (Orr & Brennan, 2016; Stockley, 2002) and the shape of the baculum (André et al., 2018; Stockley, 2012) are associated with greater sperm competition. Although human males have neither penile spines nor bacula, the shape of the human penis may similarly function as an adaptation to sperm competition. Specifically, the relatively greater penile girth (compared to humans' closest primate relatives) and the protrusion of the coronal ridge may function to displace semen already present in the female reproductive tract (Gallup et al., 2003). That is, during intromission with a woman who has recently copulated with another man, the size (girth) and shape (prominent coronal ridge) of the human penis may function to push the rival male's sperm out of the female's reproductive tract. This would function as a valuable sperm competition tactic, as sperm that have been removed from the reproductive tract are no longer viable for fertilization, giving an advantage to the man who is doing the displacing over the male whose sperm has been displaced.

Behavioral evidence supports the hypothesis that semen displacement is a sperm competition tactic in humans. Men are more likely to engage in copulatory behaviors that facilitate displacement of rival semen when the risk of the presence of rival semen is higher. For example, men whose female partners have spent more time around rival males report greater sexual interest in their partners and greater distress following their partner's sexual rejection (DeLecce et al., 2017) and report copulatory behaviors that include deeper thrusting and a greater number of thrusts (Pham et al., 2017). A similar effect is evident among men who find themselves at greater risk of sperm competition given their partner's attractiveness and other individual difference traits related to an increased risk of a partner's extra-pair sex (Goetz et al., 2005). As these copulatory behaviors, including increased thrust frequency and deeper thrusting,

have been demonstrated to displace comparatively greater amounts of semen (Gallup et al., 2003), the association of these behaviors with circumstances under which men are at greater risk of sperm competition further supports the role of semen displacement as an evolved response to sperm competition.

Of course, semen-displacing behaviors function to remove *any* semen currently in the female reproductive tract, even if that semen is one's own. As behaving in ways that could result in self-semen displacement would be disadvantageous, it would be reasonable to hypothesize that men may have adaptations to reduce the risk of self-semen displacement (Gallup & Burch, 2004). Indeed, such behaviors and physiological features have been documented. For instance, shortly following ejaculation, human males experience a significant loss of erectile volume, engage in reduced thrusting, and withdraw the penis from the vagina (Gallup et al., 2006), all of which are contrary to semen displacement and may function to reduce the likelihood of displacing one's own semen. It also has been argued that the postejaculatory refractory period, or the inability to achieve erection for some period of time following ejaculation, may function to reduce self-semen displacement (Gallup & Burch, 2004). If one cannot achieve the erection necessary to successfully copulate again following a successful copulation, then one is not at risk of inadvertently displacing one's own previously deposited semen. The fact that refractory periods are not immutable and may be overcome by the introduction of a novel female (i.e., the Coolidge effect; Vance & Shackelford, 2021) is suggestive of the functional value of such a refractory period in terms of reducing self-semen displacement.

Sperm Quality and Ejaculate Adjustment

In comparison to ova, sperm and seminal fluid are relatively inexpensive to produce in terms of metabolic expenditure (Hayward & Gillooly, 2011). However, *relatively inexpensive* does not mean *inconsequential*, and males are not expected to be indiscriminate in this expenditure. Rather, males are expected to adjust this expenditure to invest disproportionately in copulations for which sperm competition risk is higher. Indeed, at a species' level, sperm competition results in increased sperm quality along several parameters, including percentage of normal sperm, acrosome integrity, and motility (Gómez Montoto et al., 2011). Similar adjustments in sperm and ejaculate quality have been documented at an individual level, as well. For example, men who produced masturbatory ejaculates in response to sexually explicit visual materials adjust that ejaculate depending on the level of sperm competition depicted in that material.

Specifically, men exposed to depictions of sperm competition produce masturbatory ejaculates with greater sperm motility (Kilgallon & Simmons, 2005). As sperm motility is positively associated with fertility (Tardif et al., 1999), producing an ejaculate with more motile sperm in the presence of sperm competition would be a valuable response to such conditions.

Other metrics relevant to the risk of sperm competition have been related to functional ejaculate adjustments. For example, high mate value men produce comparatively high-quality ejaculates, but only when produced in response to highly attractive women (Leivers et al., 2014). Given that highly attractive women are perceived to be particularly attractive as short-term mates (McDowell & Starratt, 2019) and are more likely to embrace a short-term mating strategy (Perilloux et al., 2013), they may represent a relatively high risk of sperm competition, at least in comparison to their less attractive counterparts. Higher mate value men are also more likely to pursue a slower life history strategy (McDowell & Starratt, 2021; Strouts et al., 2017) and, given that a slower life history strategy is associated with an increased focus on a long-term mating strategy and the consequential increased risk of sperm-competition-caused cuckoldry, men who report slower life history strategies also produce higher-quality ejaculates (Barbaro et al., 2019). In short, it is possible that men who find themselves at greater risk of sperm competition by forming long-term partnerships, and at greater risk of particularly high costs of sperm competition by forming partnerships with highly attractive women, may solve the adaptive problem of increased risk by producing high-quality ejaculates likely to be successful in sperm competition.

Beyond the influence of long-term versus short-term mating strategies and the attractiveness of one's partner, there are specific copulatory behaviors men perform that may affect ejaculate quality. In general, these copulatory behaviors may function to increase ejaculate quality by increasing male sexual arousal (Pound et al., 2002). One of the behaviors that may serve this purpose is the performance of cunnilingus, a behavior associated with increased sexual arousal in men and increased duration of subsequent copulation, both of which are associated with signals of increased ejaculate quality such as ejaculate volume (Pham et al., 2016; Pham et al., 2013b). That is, men who perform oral sex on their partner may also experience increased sexual arousal and spend more time in copulation, which leads to the production of high-quality ejaculates (e.g., greater sperm number and faster sperm swimming speed) that presumably fare better in sperm competition.

Copulation Frequency, Sexual Coercion, and Forced Copulation

In addition to displacing rival semen and increasing ejaculate quality, males also may increase their chances of success in sperm competition by increasing the frequency of copulation with their partner. Indeed, men whose female partners spend more time around rival males—a circumstance that creates more opportunity for a woman to put her partner at risk of sperm competition—report greater in-pair copulation frequency, primarily when those women are perceived to be particularly attractive (Pham et al., 2014). The value of this increased copulation frequency may be twofold. First, as copulation frequency is positively related to relationship satisfaction (McNulty et al., 2016) and relationship satisfaction is negatively related to female extra-pair sexual activity (Atkins et al., 2001), it is possible that this increased frequency of in-pair copulation reduces the risk of sperm competition by increasing relationship satisfaction and consequently reducing the risk of a woman engaging in behaviors that would put her partner at risk of sperm competition.

Second, frequent copulations may decrease the likelihood that, should a female partner have engaged in an extra-pair copulation, the rival males' sperm will have an unchallenged chance at fertilization. This value of frequent in-pair copulation is evident in men's insistence on and persistence in pursuing copulation with a partner whom they believe may have engaged in extra-pair sexual activity. That is, men who are at greater risk of sperm competition are more likely to employ sexual coercion against their partners (Goetz & Shackelford, 2006; Lopes et al., 2019; Starratt et al., 2008). Additionally, following cues to increased sperm competition risk, men are more likely to report decreased copulatory duration (Barbaro et al., 2015). By engaging in forced in-pair copulation and reducing the amount of time to place his sperm in competition with any rival male sperm in his partner's reproductive tract, a man would be reducing the likelihood of cuckoldry should his partner's behavior have put him at risk of sperm competition (Shackelford et al., 2006). The reduced copulatory duration described here and the increased copulatory duration subsequent to increased cunnilingual duration described above may represent two distinct sperm competition tactics, with the former more likely to serve as a "corrective strategy" and the latter as a "preventative" strategy (Barbaro et al., 2015).

Partner-directed violence that is not specifically sexual also may function as a response to sperm competition, as female-directed violence positively correlates with frequency of in-pair copulations. That is, men who are more violent toward their partners also secure more copulations with those partners (Barbaro &

Shackelford, 2016). That said, the nature of the violence may be tailored to different aspects of sperm competition risk. For example, while men who accuse their female partners of having been unfaithful are more likely to sexually coerce their partners, men who find their partners to be already pregnant switch from sexual violence to nonsexual physical violence (Burch & Gallup, 2020). In other words, when the risk is that a female partner's behavior may have put a man at risk of sperm competition, he is more likely to engage in partner-directed sexual violence, which could function to place his sperm in competition with any existing rival males' sperm. However, when a partner's pregnancy is confirmed and the risk escalates from one of potential sperm competition to potential cuckoldry, men's behavior may shift from specifically sexual violence to nonsexual physical assault, which may more directly address the potential risk of his partner giving birth to a rival male's offspring (i.e., by causing miscarriage). Some evidence even suggests this nonsexual physical violence may be particularly targeted toward the pregnancy, with assaults to the abdomen and the developing fetus (Valladares et al., 2005).

These behavioral responses to sperm competition risk are expressions of men's evolved psychology designed to address such risk. That is, as men's risk of sperm competition increases, so too does their sexual interest in their partner, distress following their partner's sexual rejection, and persistence in pursuing sex with their partner following her sexual rejection (Shackelford et al., 2007), particularly when they perceive themselves to be at risk of a partner's infidelity (Starratt et al., 2013). Men at an increased risk of sperm competition also demonstrate increased mate-guarding behaviors, which function to reduce the likelihood of a partner engaging in behavior that would put a man at risk of sperm competition (Starratt et al., 2007). In short, men who perceive themselves to be at risk of sperm competition experience jealousy and emotional distress, which are amplified by a partner's sexual rejection and which motivate men to tenaciously pursue copulation with their partners, occasionally to the point forced sex.

Female Role in Sperm Competition

Men's sensitivity to a partner's sexual rejection and motivation to respond to that rejection with increased sexual persistence may be warranted in terms of risk of sperm competition. This is because women who have had sex with an extra-pair man may be likely to subsequently attempt delaying sex with their in-pair partner (Gallup et al., 2006). Such a delay would effectively prevent a woman's in-pair partner from successfully addressing this greater risk of sperm

competition. This behavior of delaying in-pair copulation following extra-pair copulation may be but one way in which women influence sperm competition for the purpose of granting reproductive preference to some men over others. In fact, evidence suggests that females employ a wide array of strategies to exert control over males' sperm competition success, strategies sometimes referred to as cryptic female choice (Firman et al., 2017).

These female strategies to influence sperm competition include both behavioral strategies, such as in-pair copulation delay, and physiological mechanisms. An example of the latter is chemoattractant moderated sperm choice, in which the follicular fluid of a particular woman differentially attracts sperm of some men over others in a manner that is independent of that woman's intentional mate choice (Fitzpatrick et al., 2020). Ova preferentially attract sperm from specific males, and the preferential treatment of those sperm appears to be independent of whether those sperm come from the woman's social partner or from an extra-pair partner. It is likely that these effects are the result of the influence of female reproductive fluid, including chemoattractants, on both sperm and seminal fluid. For example, female reproductive fluid can affect sperm motility, longevity, and capacitation and can influence seminal fluid such that it is more conducive to sperm viability (Gasparini et al., 2020).

It has also been suggested that female orgasm may function as a means of cryptic female choice via ejaculate manipulation, such that more sperm are retained in the reproductive tract when female orgasm occurs shortly before, during, or a brief time after male ejaculation (Baker & Bellis, 1993). Women who orgasm shortly before or less than an hour following male ejaculation, according to this hypothesis, retain more sperm from that ejaculate. That women are more likely to experience orgasm when their male partners are more attractive (Shackelford et al., 2000) and display lower fluctuating asymmetry (Thornhill, Gangestad, & Comer, 1995), two indicators of high mate value, suggests that women may preferentially retain sperm from particularly high value men. Retaining a greater portion of sperm from higher-quality men, of course, would subsequently increase the likelihood of successful fertilization by those more valuable men.

If female orgasm functions as a mechanism of cryptic female choice, then we might expect men to demonstrate interest in ensuring a female partner's orgasm, particularly when they are at greater risk of sperm competition. Indeed, evidence suggests that this is the case. For example, interest in a partner's orgasm is positively related to risk of sperm competition, particularly for men who are more highly invested in their long-term relationship (McKibbin et al., 2010). That is, men who perceive themselves to be at some risk of sperm competition

and who are invested in maintaining a relationship with their current long-term partner are more likely to report an interest in ensuring their partner's copulatory orgasm, thereby potentially increasing their likelihood of successfully surviving sperm competition and decreasing the risk of suffering the negative effects of cuckoldry. This is not to suggest, however, that any potential value of female orgasm is restricted to its purported role in cryptic female choice. It also has been argued that female orgasm may function as a broader mate-retention strategy, such that women in relationships with men who demonstrate an interest in female orgasm and pursue behaviors to that end may remain more invested in and less likely to stray from those relationships (Pham et al., 2013a). In either case, men who are more successful in ensuring their female partner's copulatory orgasms may be at a reduced risk of encountering sperm competition and/or an increase likelihood of "winning" such a competition.

Impact and Influence of Sperm Competition

Although there remains some debate as to the level of risk of sperm competition in humans, the preponderance of evidence indicates that it has played an influential role in the evolution of human sexual physiology, psychology, and behavior. As the sex subject to both the negative consequences of losing sperm competition and the benefits of winning sperm competition, men have evolved physical adaptations that function to increase their chances of successfully navigating a high risk of sperm competition and psychological adaptations that motivate behaviors both for avoiding sperm competition and for being successful when it either cannot be avoided or when it would be reproductively valuable. On the other hand, as the sex that could almost invariably benefit from sperm competition, women have adaptations for both encouraging sperm competition among rival males and ensuring that the most valuable of those rivals is successful.

Table 23.1 Proposed Adaptations to Sperm Competition

Adaptation	Function
Precopulatory	
Large testes to body mass ratio	Larger testes produce larger ejaculates, which increase chances of successful fertilization
Penis morphology (e.g., coronal ridge protrusion)	Displacement of rival male semen from the female reproductive tract
Response to a partner's sexual rejection	Increased sexual interest, persistence, and distress following rejection increases likelihood of placing sperm in competition with potential rival sperm

Sexual coercion	Increases likelihood of placing sperm in competition with potential rival sperm
Mate guarding	Prevent partner from engaging in behavior that would increase risk of sperm competition
Copulatory	
Copulatory frequency	Increases likelihood of placing sperm in competition with potential rival sperm
Copulatory duration	quickly placing sperm in competition with potential rival sperm
Increased thrusting depth and frequency	displacement of rival male semen from the female reproductive tract
Ejaculate adjustment	Ejaculate quality increases with the risk (high risk) and costs (high partner quality) of sperm competition
Chemoattractant moderated sperm choice	Cryptic female choice; female reproductive fluid preferentially attracts sperm from specific males
Female orgasm	Cryptic female choice; increased retention of sperm from high value males
Interest in ensuring female orgasm	Increase chance of preferential retention of own sperm over potential rival male sperm
Postcopulatory	
Female-specific refractory period	Reduce risk of self-semen displacement
Female-delayed in-pair copulation	Following extra-pair copulation, delaying in-pair copulation favors rival male sperm
Partner-directed nonsexual violence	Reduce risk of partner giving birth to rival male's offspring

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CHAPTER 24

Violent Mates

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Abstract

The optimal fitness outcomes of mating relationships often differ for men and women, resulting in conflict. Selection favored diverse tactics in both sexes capable of moving the fitness optima in their favor, ranging from altruism to violence. Our ancestors addressed some adaptive problems of human mating with cost-inflicting, even violent tactics. The adaptive problems include mate poachers, sexual infidelity, conflict over resource allocation, mate value discrepancies, relationship termination, and mate reacquisition. Violence directed toward mates is highly context dependent. Myriad situational factors affected the fitness costs and benefits of mating violence, selecting for context-sensitive psychologies and tactics in aggressors to manipulate victims and co-evolved victim defenses to avoid or minimize their victimization.

Key Words: sexual conflict, infidelity, mate poaching, relationship termination, intimate partner violence

The fitness consequences of heritable traits shape them. For example, the circulation of blood is the evolved consequence of a beating heart. Genes that code for the reliable development of adaptations are under constant selection, favoring improved functional consequences—outcomes that more precisely address adaptive problems and ultimately advantage the genes' rate of replication relative to alternative alleles.

Most behaviors are the evolved consequences of adaptations. Like physiological adaptations, these behaviors were ancestrally functional in contributing to the replication of the genes that directed their development in

individuals across generations. However, it can be more difficult to make direct connections between behaviors and their evolutionary origins, especially when similar-looking behaviors are employed in different situations and have different effects. In these cases, the evolved functions of behaviors can sometimes be understood by identifying corresponding ancestral problems in which the context-specific consequences of the actions delivered fitness benefits. For example, the unrequited desire to rekindle a lost long-term mateship could be addressed with acts of kindness or acts of violence. For reasons that will be discussed, acts of kindness are likely superior to acts of violence in winning back an ex-mate. In certain contexts, however, violence may be the best option available.

There are numerous sources of conflict in contexts of human mating, many stemming from men's and women's competing fitness interests. The conflicts can be resolved in a variety of ways. Providing mates with benefits such as pleasure and money can induce their reciprocal investment (Buss, 1992). Cost-inflicting strategies are also used, such as the extortion of resources by threatening relationship integrity (e.g., jealousy induction) or holding back relationship benefits (e.g., resource or sexual withholding); deception (e.g., concealing financial status and feigning pregnancy); coercion (e.g., threatening desertion and pressuring for more commitment), intimidation (e.g., making threats and other psychological abuse); and violence, sexual violence, and homicide (Buss, 1992; Buss & Duntley, 2008, 2011; Frieze, 2005).

Sexual Conflict Theory

Humans are rare among species in forming monogamous pair bonds and providing biparental care for offspring, a mating system which exists in only 3 to 5 percent of mammalian species (Kleiman, 1977). There are large potential benefits from long-term mating for both women and men. The benefits women gain include physical protection for themselves and children; an additional source of food and other provisions; and a partner in parenting, teaching, socializing, and influencing the future trajectory of children (Hill & Hurtado, 1996). Men who mate long-term obtain benefits that include attracting more desirable mates, greater sexual access, more physical proximity for mate guarding, greater paternity certainty, increased survival of children, and added support through alliances with a mate's kin (Buss, 2019; Buss & Schmitt, 1993).

With the great benefits of mutualistic strategies in long-term mating for both sexes, the possibility of violence between partners can seem counterproductive or implausible. But in the United States, approximately one in four women and

one in seven men will experience physical violence perpetrated by their intimate partner at some point in their lives (Huecker & Smock, 2020). More than ten million people are victims of intimate partner violence in the United States each year. Although most is minor, such as grabbing, shoving, slapping, and hitting, serious injuries and homicides do occur. The lifetime likelihood of women being battered by an intimate or ex-intimate is estimated to be between 25 and 30 percent in the United States, with some studies placing the prevalence as high as 34 percent (Frieze et al., 1980; Huecker & Smock, 2020; McHugh & Frieze, 2006). Fifty percent of women seen in emergency departments report a history of domestic violence. Violence affects roughly 325,000 pregnant women each year, causing up to 10 percent of pregnant hospital admissions. Forty percent of women killed by their abuser sought help in the two years before their deaths (Huecker & Smock, 2020).

About one in five women in the United States will experience a completed or attempted rape in their lifetimes (Smith et al., 2018). It is estimated that between 10 and 14 percent of all married women in the United States have experienced rape at the hands of their intimate partner (Martin et al., 2007).Cross-cultural estimates of marital rape range from 10 to 26 percent (Kaighobadi et al., 2009). Most victims do not seek help (Huecker & Smock, 2020). Psychological and emotional abuse are not included in these figures but are likely more common (Buss & Duntley, 2011). It is clear that many men seek to control their mates, often with violence. Sexual conflict theory can explain why.

For much of the history of the fields of psychology and biology, long-term mating relationships were assumed to be cooperative, harmonious alliances between males and females that functioned to produce and raise offspring (Parker, 1979). Far from natural, conflict in human mating relationships was, and often is, viewed to be a sign of relationship pathology requiring treatment in couple's therapy (e.g., Gottman, 1999). Work by Parker (1979, 2006) transformed our understanding of mateships, explaining that predictable forms of conflict between partners arise naturally from conflicts in the evolutionary interests of the two sexes. Fitness optima can differ for men and women (Buss, 1996), especially in contexts of human mating where the sexes differ in minimum obligatory parental investment (Trivers, 1972) and the certainty of genetic relatedness to offspring (Scelza et al., 2020). Selection will favor adaptations in individuals of each sex to move the behavior of the other sex closer to its own optimum. The resultant conflicts are between individual males and individual females and not the sociological monoliths *males as a group* and *females as a group*, which are not tenable levels of natural selection (Buss, 1996; Williams, 1966). Individual men do often work to maintain exclusive province

over women's sexuality but are primarily in competition with their intrasexual rivals, just as women's primary competitors are other women for the same mates and mating resources (Wilson & Daly, 1992).

Conflicts between the sexes created by ancestrally recurrent differences in the fitness optima of men and women led to coevolutionary arms races, similar to those between predators and prey. For example, an offensive adaptation in males that moves female's behavior closer to the male fitness optimum imposes costs on females and creates selection pressure for coevolved female defenses. The coevolved defenses move the optimum back in females' favor, creating new selection pressure on males to counter with their own new offensive adaptations to defeat females' new defenses. Such coevolutionary arms races will continue in perpetuity, until natural constraints end them (Buss & Duntley, 2011; Duntley, 2015).

Conflict between the sexes can be conceptualized in terms of the stage of the relationship in which it occurs—before mating during courtship, during the mateship, and after a breakup (Buss, 2017). In the courtship stage of a relationship, there can be sexual conflict about the timing of first sexual intercourse and the amount of investment that precedes it. Men commonly use deception and sexual persistence to try to get sex sooner and with less investment than is optimal for women (Buss, 1989a, 2017; Haselton et al., 2005). To move the male optimum in their favor during courtship, women often deflect sexual attention, create time delays between dates or meetings, and require honest signals of commitment. During the mateship, conflict between men's and women's optima can emerge in the frequency of sex, acquirement and allocation of resources, investment in "in-laws," relative investment in parenting, and mating effort outside the relationship. Sexual conflict frequently continues even after a breakup (Duntley & Buss, 2012a, b).

Ex-mates, most often the lower mate value partner and the one who was rejected, may seek to rekindle a long-term relationship or retain a sexual relationship with their former partners, often trying to prevent their former partners from starting new relationships (Duntley & Buss, 2012a). This form of mating conflict leads over a million women to report being stalked each year in the United States (Breiding et al., 2014), with some researchers estimating that 49 percent of people are stalked in their lifetime (Bjorklund et al., 2010).

Through the lens of sexual conflict theory, we can see that conflict between the sexes is common and predictable. Far from being dysfunctional or pathological, sexual conflict is the natural product of evolved conflicts in the fitness interests of males and females, which have their origins in biological differences in their contributions to reproduction (Buss, 2016; Daly & Wilson,

1983). Conflicts of human mating pervade all stages of mating relationships, from courtship onward. That these conflicts are natural does not make cost-inflicting tactics to resolve them acceptable or morally justified. An evolutionary approach to understanding sexual conflict can help us to recognize and understand the mating domains that are most dangerous and develop interventions to address them.

Men and women in mateships can benefit from cooperating with each other (Cronin, 2006). Pregnancies are healthier with supportive mates (Stapleton et al., 2012). Children with two investing parents are more likely to survive and thrive (Geary, 2016; Mattison et al., 2014; Shenk & Scelza, 2012) and may have greater reproductive success (Lynch & Lynch, 2017). Cooperation is greatest in conditions of strict monogamy, no stepchildren, and no in-laws who could lead to conflicts in resource allocation (Daly & Wilson, 1988). But strict monogamy is rarely if ever achieved in human mateships. Partners may cheat or otherwise invest resources to cultivate alternative mating prospects. Relationships may dissolve. Partners may battle over equitable investment in parenting, stepparenting, and extended kin. For humans, sexual conflict is pervasive.

The Evolution of Violent Mates

The seminal work of Daly and Wilson (1983, 1988,) opened the door to examining the evolutionary underpinnings of coercion and violence in human mateships. They used the concept “male sexual proprietariness” to describe men’s adaptations to the ancestrally recurrent threats of women’s sexual infidelity or defection to a different male partner. Rather than being an aberrant and unpredictable expression of male hostility, Wilson and Daly (1996, 1998) explained that men’s psychology of sexual proprietariness was activated by environmental cues ancestrally predictive of loss of sexual control or access to their female partner. Using violence to prevent infidelity and relationship defection is a risky strategy, which can cause men to lose their relationship entirely or suffer retribution, sometimes violent, from women’s kin and social allies. The presence of these risks can decrease men’s violent control of their partners.

Men’s violence controls women sexually and socially. It deters women from cheating and sexual rivals from mate poaching, and it restricts women’s ability to find or even seek outside social support or other mates (Buss, 2000; Wilson & Daly, 1996). Although obviously costly for women—injuring them, restricting their freedom of mate choice, and hampering their ability to invest in other key adaptive problems—men who were coercive and violent in response to threats to

their partner's monogamy would have gained paternity certainty and increased their reproductive success.

Fundamentally, all mating conflicts involve the diversion of mating resources to individuals outside the mateship. Adaptations that evolved to stanch the loss of resources produce behaviors that range from vigilance to violence, shaped by the ancestral costs and benefits of the tactics (Buss, 1988; Buss & Shackelford, 1997; Shackelford et al., 2005; Wilson & Weghorst, 1982). Nonviolent tactics, such as stable resource provisioning and sexual enticements, likely prevent the majority of mating resource diversion (Buss, 2000). But the arsenal of tactics also includes threats of aggression, abandonment, defection from the relationship, and physical violence.

Violence is only one among many possible tactics that evolved to solve adaptive problems of conflict between mates. The large, even lethal possible costs that perpetrators of mating violence can suffer from their victims and the victims' defenders suggest that violence should only be employed in contexts where the likelihood of incurring costs is low, the magnitude of the fitness threat without a violent response is critically high, or both. We will find violent mates in these adaptive problem contexts, which include: the loss of resources intrinsic to the relationship with a partner, threats to those resources, and partners who fail to deliver fitness-critical benefits consistent with the social contract of the relationship (Buss & Duntley, 2011).

Adaptive Problems That Lead to Mating Violence

The adaptive problems faced before, during, and after a mateship are multiple and complex. Exploring the nature of these problems will allow us to identify when violence was the favored solution for solving them. This chapter focuses on male violence against women because men are many times more likely than women to adopt such extreme measures (Archer, 2002; Daly & Wilson, 1988; Figueredo et al., 2012). Women can be violent as well, although they typically inflict less damage (Archer, 2002; Walker et al., 2019; Williams et al., 2008). Any complete theory of mating violence should address violence perpetrated by women in addition to the violence of men (Frieze, 2005).

Mate Poachers

Mate poachers seek to start relationships with people who are already in a relationship with someone else. Mate poaching is an unexpectedly common strategy to acquire a mate (Schmitt & Buss, 2001; Schmitt et al., 2004).

Research in the United States found that 93 percent of men and 86 percent of women admitted to trying to lure someone out of an existing relationship to start one with them (Schmitt & Buss, 2001). Attempting to poach someone for a short-term sexual affair was almost as common, with 87 percent of men and 75 percent of women reporting it. There is cross-cultural variability in the prevalence of mate poaching, but the vast majority of people have experienced it in some way: as a mate poacher, as an object of mate poaching, or having a partner who is a mate poacher or object of mate poaching (Schmitt et al., 2004). One reason for the high rates of mate poaching may be that many of the best mates have already been chosen for long-term relationships. It is clear that by strategically interfering with a long-term relationship or successfully seducing someone away from their partner mate poaching is a daunting adaptive problem for the survival of long-term relationships. Indeed, lovers' triangles are toxic sources of violence and homicide (Shackelford et al., 2003), especially in people's professional lives, where they are the most common cause of workplace homicides (Geldenhuys, 2017; Lavender et al., 2016).

Consistent with evolutionary logic, the most threatening mate poachers are those who can offer a better source of the characteristics most desired by the opposite sex. For men, poachers with more financial resources, better careers, and greater physical formidability are particularly threatening (Buss et al., 2000; Davies & Shackelford, 2015, 2017). Rivals with more beautiful faces or bodies are particularly threatening to women. Sex differences in distress about rivals with these characteristics have been found in the United States, Korea, and the Netherlands (Buss, 2000).

When faced with the adaptive problem of mate poaching, men more often respond violently toward poachers than toward their mates (Wilson & Daly 1988). Female victims of intimate partner violence are more likely than nonvictims to characterize their partners as jealous, controlling, and trying to isolate them from friends, family, and other social contacts (Wilson & Daly, 1996). The result is that men's use of violence can limit their partner's exposure to other men and potential mate poachers.

Sexual Infidelity

A woman's sexual infidelity may lead her long-term mate to invest in children that are not genetically his, benefiting the fitness of a male rival at a cost to cuckolded man (Buss, 2000; Daly et al., 1982; Symons, 1979). For a man whose partner cheated, even the time his long-term mate spends pregnant with another man's child represents months of lost reproductive opportunity with the

potential for years more due to lactational amenorrhea. Although women do not experience uncertainty in their genetic relatedness to their offspring, they too incur costs from sexual infidelity by the men who are their long-term mates in the form of diverted investments of time and resources to another woman. Emotional involvement with an affair partner, which an estimated 70 percent of women and 35 percent of men experience (Glass & Wright, 1985, 1992), increases the likelihood that men and women will ultimately choose to be with them.

Violence is one tactic among many that men use to address the adaptive problem of their partner's infidelity. Among the best predictors of intimate partner violence is suspicion or detection of a cheating partner. A powerful study of battered women (Shields & Hanneke, 1983) compared a group of women who were both raped and beaten by the husbands to another group of women who were beaten but not raped by their husbands. The control group consisted of nonvictimized married women. Women in all groups were asked if they ever had sex with another man while living with their husband. Of the women who answered yes, 47 percent were in the group of women who were both battered and raped, 23 percent were in the group who were battered but not raped, and 10 percent were in the control group of nonvictimized women. The study provides clear evidence that women's sexual infidelity may increase their risk of being physically and sexually assaulted by their long-term partners.Other research in the United States shows that male violence leading to injury and forced intercourse are more common in married couples than in dating couples (Krienert & Walsh, 2018). Married men's greater relationship investment may make their partner's infidelity more costly. Although we cannot determine conclusively whether women's infidelity led them to be abused or their partner's abuse led women to be unfaithful, the findings are consistent with the evolutionary argument that the high costs of paternity uncertainty associated with women's sexual infidelity is an adaptive problem with fitness consequences great enough to select for violence as a possible adaptive solution.

Men's sexual coercion or rape of their long-term partners also appears to be a consequence of the suspicion or reality of the women's sexual infidelity (Goetz & Shackelford, 2009; Goetz et al., 2008a; Russell, 1982). Research has found that men are more likely to rape (Camilleri, 2004) or sexually coerce (Goetz & Shackelford, 2006) female partners they perceive to be unfaithful (Camilleri & Miele, 2016). Studies of convicted partner rapists have produced similar findings (Camilleri & Quinsey, 2009).

Two hypotheses have been advanced to explain these findings. The first is that men sexually coerce and rape to enable their sperm to compete with the

sperm of a rival to fertilize their partner's egg (Goetz et al., 2008b; Shackelford et al., 2016). The second hypothesis is that sexual coercion is the product of men's desire to dominate and control women (Brownmiller, 1975). These two explanations are not necessarily incompatible (Goetz et al., 2008b). Men may use physical dominance to sexually coerce female partners in order to increase their odds of paternity. A chance at paternity through sperm competition would deliver better fitness outcomes than if men did not compete at all. And counterintuitively, it may be the men who perceive their female partners to be the most valuable, the most irreplaceable, who are most motivated to risk employing violent tactics to retain them.

Genetic Cuckoldry

When a man's mate becomes pregnant with a rival's child, the solution can no longer be to prevent her sexual affair. Instead, when violence is used, its hypothesized function is to end the life of the rival's offspring by terminating the pregnancy. This would allow a female partner to conceive with her long-term mate sooner and free her parental resources for existing and future children with him (Friedman & Shackelford, 1999).

Although this hypothesis has not been tested directly, growing evidence supports it. One study found that partner violence toward pregnant mates occurred at twice the rate of violence directed toward nonpregnant partners (Burch & Gallup, 2004). The men in the study who were violent toward their pregnant partners were more likely to be characterized as experiencing sexual jealousy, which has been identified as the variable most strongly associated with severe physical victimization by other researchers (Hellmuth et al., 2013). Other studies found more direct evidence, finding that pregnant women who were abused were indeed more likely to be carrying another man's child (Martin et al., 2004; Taillieu & Brownridge, 2010).

Following the battery of pregnant women, the fetus is at greater risk of adverse pregnancy outcomes, such as miscarriage, stillbirths, and premature delivery (Bhole et al., 2014; Bullock & McFarlane, 1989). Pregnant abuse victims are more likely than nonpregnant women to have multiple sites of injury (Helton, 1987), and they are also more likely to be struck in the abdomen (Bhole et al., 2014; Bohn, 1990). Research conducted in Nicaragua found that about 50 percent of pregnant women who were victims of intimate partner violence suffered blows to their stomachs (Valladares et al., 2005). A similar finding was obtained in research on pregnant women in the Abay Chomen district of Western Ethiopia (Abate et al., 2016). Injury to the placenta or directly to the fetus can

occur with minor maternal injuries, resulting in the death of the fetus (Pearlman et al., 1990).

Other research found that the babies of pregnant women who were abused are more likely to be born preterm, low birth weight, and small for their gestational age (Chisholm et al., 2017; Donovan et al., 2016; Hill et al., 2016), a finding replicated in Tanzania (Sigalla et al., 2017) and Vietnam (Hoang et al., 2016). These are all outcomes that would decrease the newborns' chances of survival, especially in the evolutionary past.

In research from Tanzania using data from the World Health Organization (WHO) Multi-Country Study on Women's Health and Domestic Violence, the evidence is even more direct (Stöckl et al., 2012). Lifetime physical and/or sexual violence from a partner was reported by 41 percent of the ever-pregnant, ever-partnered women in Dar es Salaam and 56 percent in Mbeya. Among abused women, 23 percent experienced involuntary pregnancy loss, a rate 1.6 times higher than among pregnant women who were not abused. Similar findings have been found elsewhere in Africa (Ahinkorah, 2021).

An actual pregnancy by another man is a somewhat distinct adaptive problem from infidelity threat. Unlike intimate partner violence that functions to deter the woman from infidelity, blows to the abdomen of a partner pregnant with a rival's child specifically function to end the life of a rival's offspring. Consistent with this, although non-pregnant women's faces, heads, and necks are targeted with violence by intimate partners more frequently than other parts of their bodies (Allen et al., 2007; Wu et al., 2010), pregnant abuse victims are significantly more likely to be struck in the abdomen (Bhole et al., 2014; Bohn, 1990).

In sum, men are more likely to be violent toward their pregnant partners when they suspect the fetus was fathered by another man, violence toward pregnant partners is more extreme when it is fueled by sexual jealousy and suspicions of lack of paternity, and the abdominal region is more often targeted in pregnant abuse victims. This can lead to fetal death, premature birth, and failure to thrive among children born to abused mothers. These findings specifically support the evolutionary hypothesis that cuckolded men may use violence to eliminate a rival's offspring, so that resources can be directed instead to their own children.

Conflict over Resources

Cooperation between long-term mates toward common goals, including pooling resources and dividing labor, can deliver significant fitness benefits to both male and female partners. Conflict can emerge when one partner perceives

that they are investing more than they are getting in return from social exchange within the relationship (Buss, 1989a, 2017). Although their long-term relationship is important to their fitness interests, investments outside the relationship can also yield fitness returns. Men may use familial resources to purchase meals and gifts for extra-pair mates, while women may invest familial resources to make themselves more sexually attractive to other men. Recent research also suggests that women may invest pooled family resources in their children well beyond diminishing returns in the pursuit of higher status among other women in the community, with the ultimate goal of benefiting their children (Cassar et al., 2016) and extended kin. With all the ways men and women can divert pooled familial resources in directions that enhance their own fitness at the expense of their partner's, it is not surprising that conflict over money is so common in long-term mateships (Buss, 2003).

Conflicts over resources are multiplied when resources are scarce. Women desire long-term partners who are able and willing to provide resources (Buss, 1989b). When men fail to provide resources during a mateship, it can eliminate a key component of attraction and lead women to experience relationship dissatisfaction. This can be compounded when men lack the ambition and industriousness to garner additional resources, two additional qualities women desire. It could be better for women whose partners are not capable of providing resources to seek a different relationship, one that offers adequate support for offspring. Losing a mate to a rival would have large negative fitness consequences for men. Without the ability to offer resources to retain their relationship, men may resort to inflicting costs, including the use of violence (Wilson & Daly, 1993). Research has documented a link between lack of economic resources and intimate partner violence in the United States (Flynn & Graham, 2010) and globally (VanderEnde et al., 2012).

Men's perpetration of intimate partner violence in conditions of economic deprivation has often been interpreted through the lens of "stress" (Flynn & Graham, 2010) or regressive "gender identities" (Gibbs et al., 2018). In the first model, economic deprivation leads people to escape in alcohol and drugs, which creates psychological stress that increases intimate partner violence. In the second model, less educated people have less gender equitable attitudes and more controlling behaviors, which increase the likelihood of partner abuse when economic resources are scarce. In contrast to these accounts, an evolutionary perspective provides a more direct and nuanced explanation, suggesting that men's failure to provide economic resources is a violation of women's evolved desires, increasing conflict in the relationship, and sometimes contributing to women's defection to other mates. Without other resort, men could use violence

as a strategy to suppress the impact of women's relationship dissatisfaction and prevent their defection. This view may be compatible with the "stress" hypothesis as it applies to men's failure to provide economic resources. Invoking the creation of more equitable gender norms as a potential solution to intimate partner violence, however, ignores both the reality that gender roles are not arbitrary cultural constructions (Geary, 2020) and research findings that show little influence of country-level gender equality on the risk of intimate partner violence (Iver et al., 2020).

Mate Value

Individuals choose long-term mates nonrandomly, preferring to select partners with characteristics similar to themselves. Mate choice for overall mate value, which is an individual's overall desirability on the mating market (Buss, 2003), is one of the strongest areas of positive assortment in human mating (Buss & Barnes, 1986; Conroy-Beam, 2017; Conroy-Beam & Buss, 2016). Generally, this means that people tend to choose long-term partners who have similar mate values to their own. However, a variety of factors can lead to relationships in which the partners differ in their mate values.

Errors of selection are one source of mate value discrepancy in long-term relationships. For example, someone might deceive a prospective mate about their prior number of sex partners or their current economic situation or potential (Haselton et al., 2005). The deceived person would end up entangled with a lower mate value partner, faced with the dilemma of staying in a suboptimal relationship or facing a potentially costly breakup. As comedian Chris Rock has pointed out, "When you meet somebody for the first time, you're not meeting them, you're meeting their representative." Another source of mate value discrepancy occurs when a partner has hidden shortcomings that are not discovered until after a couple has committed to a relationship. A woman might be secretly in love with someone else, and hoping for an opportunity to be with him. A man's parents could be raising his child from a previous relationship as their own. Both sexes may be able to conceal other undesirable characteristics during the courtship stage of the relationship, which may not emerge until the partners have committed to each other. They include personality or psychological disorders, health issues, toxic relationships with close family members, and sexually transmitted diseases. The additional costs associated with these deficiencies can substantially increase the relationship load that the higher value partner must endure (Buss, 2006).

Mate value discrepancies can also be a product of partners forming long-term

relationships when they have not yet accurately recognized their true mate value. This may occur, for example, between high school sweethearts who have not received much feedback from others about their desirability. Relatedly, a person of high mate value may be relatively isolated in a population of potential mates with lower mate values. Even if they partner with the best of the available mates in the population, a discrepancy will still exist and may only be discovered through eventual interactions with other populations of people. Finally, mate values may change over time in a long-term mateship, creating discrepancies that did not exist at the relationship's inception. As years pass, a partner could experience incredible career success, suffer a debilitating injury, or develop a chronic disease, creating new, unforeseeable mate value discrepancies. Mate value is a composite of many characteristics, most of which are likely to change over time. It is actually quite likely that the mate values of couples who are well-matched at the beginning of their relationships will diverge over time (England & McClintock, 2009). Even without a personal boom or bust, women decrease in mate value as they age and their reproductive value decreases. During that time, men's mate values can increase or decrease through the accumulation or loss of resources or social status.

Mate value discrepancies may contribute to intimate partner violence, especially when the female partner is substantially higher (Buss & Duntley, 2011), a condition in which women have been shown to have low relationship satisfaction (Nowak & Danel, 2014). Higher female mate value may contribute to the activation of several evolved psychological programs for mate retention in their male partners. Higher mate value partners are (1) more likely to have sexual affairs (Buss, 2000; Buss & Shackelford, 1997), (2) more likely to attract mate poachers, and (3) more likely to produce cues of potential relationship defection. In addition, the lower mate value male partner will struggle to provide additional investment and other enticements to prevent the woman from believing she could do better, making her more likely to cheat or leave him. Studies have shown that lower mate value partners are more controlling and aggressive (Danel et al., 2017; Graham-Kevan & Archer, 2009), and that mate value discrepancies can contribute to abuse (Bhogal et al., 2019).

In long-term relationships with mate value discrepant partners, violence against the higher value partners can function to adjust their calculus of the costs of straying or defecting (Wilson & Daly, 1993). Being a victim of mating violence can also decrease people's perceptions of their own mate value, effectively reducing the magnitude of the mate value discrepancy. Research suggests that mate value is a component of self-esteem (Kirkpatrick & Ellis, 2001), which can be devalued when a person is a victim of psychological,

physical, or sexual abuse (Kaura & Lohman, 2007; McHugh & Frieze, 2006; Russell, 1982; Straight et al., 2003). Female victims of abuse may come to believe that they are unattractive and undesirable, and that their abusive partner is the best they can do. Further, abusive men can actually make their partners less attractive to rivals by lacerating and bruising their faces. It is possible that visible wounds to a woman's face function as a signal that male rivals should stay away; the woman is mated to someone who can deliver violence with impunity or has little to lose. Although abhorrent, mating violence may ultimately function to deter infidelity and retain mates in contexts of mate value discrepancy.

Relationship Defection

The end of a mateship also represents a substantial decrease in access to a partner's reproductively relevant resources. Often, a relationship's end means the complete loss of all such resources. Divorce can be financially devastating for mothers and children in the United States (Tach & Eads, 2015), with household incomes 33 percent lower after divorce. However, women in very low-quality marriages have been found to gain life satisfaction after divorcing (Bourassa et al., 2015). Men who lose a female partner will lose access to all of her residual reproductive value, from which a male rival can benefit (Duntley & Buss, 2011). For the rejected partner, the benefits of trying to keep the relationship together can be substantially greater than any other available options, selecting for adaptations to prevent mates from defecting (Buss & Duntley, 2011).

The social reputations of those who end relationships can also be damaged by a breakup, especially for the person who is rejected. People are less likely to desire a romantic relationship with someone who was rejected by their previous partner (Stanik et al., 2010), making it more difficult for previously rejected mates to attract someone new. As argued by Buss (1988) and Buss and Shackelford (1997a), solutions to the problem of mate defection can range from vigilance to violence. People who are rejected by their long-term partners have been found to direct behaviors at their ex-mates that include physical threats, stalking, and violence (Perilloux & Buss, 2008). These tactics may not be effective in retaining a mate who is attempting to defect in the majority of cases (Delecce, 2017), but they don't have to be. Selection will favor a tactic, even if it provides as little as a one percent advantage over alternatives in a given context (Nilsson & Pelger, 1994).

Unfortunately, women do sometimes stay with abusive partners. If they leave, they are frequently soon to return. Intimate partner violence is part of the lives of

roughly 25 percent of women (Huecker & Smock, 2020), comprising roughly 15 percent of all crimes in the United States in 2011 (Truman & Planty, 2012). Thirty-six percent of female victims suffer from multiple different forms of violence (Breiding et al., 2014). In a study of 150 women and their children at a shelter for battered women, 52 indicated that they returned to their abuser (McFarlane et al., 2015). Women who returned experienced a higher level of violence and mental health problems than women who did not return. Another study of 100 women found that about 27 returned to their partners after the men promised they would change and no longer be violent (Gayford, 1975). Seventeen others returned because their partner threatened further violence. Of the remaining women, fourteen returned because they needed a place to stay, thirteen returned because they thought it was better for their children, and eight returned because they indicated they were in love or felt sorry for their abuser. Similar findings were obtained in a comparison of younger and older battered women (Eisikovits & Winterstein, 2015). Eisikovits and Winterstein (2015) found that women who stayed with their abusers experienced isolation, bodily pain, estrangement, alienation, and loneliness—all indicative of abusers who were successful in isolating their victims from sources of social support to better control their behavior.

One seventy-eight-year-old woman reported, “Fifty years went by. I lost my whole life. He made me into an imbecile. When I needed to buy something for the children or for myself, I had to ask him for money and he made me bring him the receipts. I have no friends, no family here” (p. 52). Another woman who was twenty-five years old said, “I always felt as if I was doing something wrong, against him…. I feel like I have been here for ages and my legs are tied to him…. I am afraid to break away. Like a baby, like a fucking baby” (p. 52).

Using violence to prevent a partner from defecting is not always successful (McFarlane et al., 2015). Most often, it drives mates away. Men’s use of violence to retain mates is a tactic of desperation for men who cannot otherwise prevent their partner’s defection, which is consistent with evolutionary hypotheses for the context-dependent adoption of mate retention tactics (Daly & Wilson, 1988; Shackelford et al., 2005). Its relative rarity and low success rate should not be confused with its fitness utility. There is clear evidence that violence can successfully function to retain some mates, giving men a longer period of access to their mates’ reproductive and relationship value.

Mate Reacquisition

Male violence can be effective at retaining mates who are threatening to leave

a relationship and even pressure some women to return after they temporarily leave, but men's aggression cannot be utilized as effectively when a mate has permanently left the relationship—when abusive men cannot directly exert their control through physical violence. Although threatening to defect from a relationship and actually leaving a relationship both involve the loss of reproductively relevant resources, preventing defection and reacquiring a lost mate have different solution sets (Buss & Duntley, 2011). Specifically, stalking behaviors seem specialized for the task of reacquiring ex-mates and are common among men whose partners have rejected them (Duntley & Buss, 2012a).

Stalking by men typically involves the repeated infliction of relatively low-level costs, such as *repeated*, *unwanted* phone calls, text messages, emails, letters, social media posts, gifts, visits, and persistent following (Duntley & Buss, 2012a). Stalkers make it clear to their victims that these unwanted behaviors will end if they give the relationship one more chance, leading many women to positively reinforce stalkers' behaviors by giving in to their demands. When these tactics are not effective, stalkers may escalate to spying on their victims (75 percent), making threats (45 percent), vandalizing property (30 percent), and even threatening to kill them or their pets (10 percent) (Buss, 2000). Stalking an ex-mate is a predictor of the likelihood the stalker will physically and sexually assault her (Duntley & Buss, 2012a). Stalkers can be especially violent when their former partners enter a mateship with someone else.

Although some stalking is the result of psychopathology and all illegal forms of stalking are reprehensible, the hypothesis that stalking behavior evolved as a solution to the adaptive problem of mate reacquisition is quite plausible (Duntley & Buss, 2012a). Patterns of stalking victimization bear this out. Women are by far the most common victims of stalking (Tjaden & Thoennes, 1998), especially young women. Most stalking victims are between eighteen and twenty-nine, and 87 percent are under forty (Buss, 2000). Their youth is not an accident. Men evolved to take greater risks in precisely the contexts that could deliver the greatest fitness gains, such as regaining access to a mate high in reproductive value (Daly & Wilson, 1983).

A range of research studies have shown that somewhere between 30 and 58 percent of stalkers are motivated by a desire to reacquire a mate who left them, often believing that they are the best person their ex-mate could end up with, even if she doesn't realize it yet (Duntley & Buss, 2012a). Mate value discrepancies can be a contributing factor to the unrequited relationship desires apparent in cases of stalking. It is the lower mate value partner who is more often rejected and more likely to resort to stalking behaviors. It is perhaps not

surprising that most stalkers are unsuccessful in winning back their ex-mates. However, about one in three stalking victims indicate that they gave into their stalker's demands (Buss & Duntley, 2010). Although they do not return to a relationship with them, some victims even have sex with their stalkers. Additionally, stalking can be very effective at interfering with victims' attempts to start new romantic relationships. There is no question that stalking is undesirable. But it is also a tactic spurned mates can use to isolate their exes long enough to obtain at least partial access to their reproductively relevant resources.

Discussion

An evolutionary perspective of violence in mating relationships allows us to make sense of why an evolved mind that produces love and longing for romantic partners can also produce conflict and violence. Sexual conflict theory tells us that romantic relationships are harmonious when partners' fitness interests align but can be suffused with conflict when they do not. Conflicts between mates occur in the form of adaptive problems, such as mate poachers, sexual infidelity, cuckoldry, conflicts over shared resources, mate value discrepancies, breakups, and the unrequited desires of spurned partners to regain lost relationships. Substantial evidence supports the hypothesis that violence evolved as one possible solution to these problems. We have explored how violence can be a functional tactic in mating relationships. How evolved psychological programs produce violence must also be discussed.

Mating Violence Is Context Dependent

Violence in mateships is not a blind instinct that builds up until it explodes. Instead, the hypothesis that violence can have evolved functions requires its use to be highly sensitive to all aspects of the situation, including personal characteristics, relationship characteristics, social influences, economic constraints, and cultural conditions. For example, men with great wealth have more plentiful nonviolent options to retain a mate (and attract other mates) so are less likely to resort to violence. Men with a slow life history strategy and greater empathy are also less likely to be violent toward mates (Buunk & Massar, 2019; Tanha et al, 2010). Being male is linked to a higher likelihood of perpetrating sexual assault and violence (Daly & Wilson, 1983; Tanha et al., 2010). In some cultures, men are less likely to batter their wives when they live closer to the wife's kin or her other social allies (Figeuredo et al., 1998). Sexual assault perpetrated by men may also be deterred when a woman has male kin nearby

(McKibbin et al., 2011). Mate value discrepancies in mateships are hypothesized to lead to greater violence in relationships and more violence directed toward mate poachers from the lower mate value partner (Buss & Duntley, 2011). The cultural influence of societal institutions, such as enforcing laws and informal community sanctions, make violent behavior more costly and affects the calculations of costs and benefits associated with the tactic (Duntley & Shackelford, 2008; Pinker, 2011). There are also other costs that perpetrators of violence are likely to incur.

Attacking another person can be very costly for the attacker. In physically defending themselves against violence, victims may injure or kill their attacker. Victims, their kin, and their social allies may also violently retaliate against attackers later (Bleske & Buss, 2001). Behaving violently toward a partner can permanently drive them away from the relationship (Delecce, 2017). Those who use violent tactics can also suffer reputational damage. Prospective mates will be wary of a man known as a "wife beater" (Burkett & Kirkpatrick, 2006). Those great potential costs to perpetrators are hypothesized to have selected for psychological design features that anticipate, minimize, and avoid them (Buss & Duntley, 2011). When perceived as too costly, violence may be abandoned entirely.

Choosing Violence

It is noteworthy that violence is a solution to a range of different adaptive problems resulting from mating conflict. Our psychological adaptations rely on numerous *contextual factors* to determine when violence is the best of available solutions. It can be useful to categorize the contextual factors that influence the adoption of a strategy as either enduring or transient. Enduring factors are those that are fairly stable over time, such as a person's physical formidability, life history strategy, and local cultural practices. Because they do not change rapidly, the values of enduring factors can be stored in our evolved programs, ready to contribute to the calculus of whether violence or some other behavior will be adopted as part of the solution for a particular adaptive problem. Transient contextual factors, in contrast, are in constant flux. They include information such as the ovulatory status of one's mate, whether she is with a mate poacher, and whether he is carrying a weapon. Transient contextual factors require fresh observations of the environment, making them more cognitively taxing to track and ascertain with as much certainty as is possible for enduring contextual factors.

It is the presence of an adaptive problem plus the right combination of

contextual factors that lead psychological adaptations to adopt one behavioral response instead of another, similar to how a specific password is needed to access a secure website or run a computer program. Each character in the password is a contextual factor. Each factor can have a range of different values. Some may be metric and others nonmetric. Only certain, specific combinations of values will activate a given evolved behavioral program.

Emotion and conscious scenario building are important design features in the function of adaptations that produce violence. A person faced with mating conflict will typically experience negative emotions. The negative emotions associated with the presence of a serious adaptive problem can be naggingly invasive of conscious thoughts, consuming the imagination with scenarios that could take place to address the situation. People are able to track changes in their emotional state associated with different courses of action and their outcomes within the fictional scenarios they create, often favoring the behavioral tactic that is imagined to provide the greatest relief from their psychological pain. Through scenario building, people can also identify ways to change transient contextual factors in their favor and minimize the impact of potentially costly enduring factors. This kind of planning could lead to dramatic shifts in the cost-benefit calculus of possible behavioral strategies.

Sexual jealousy is a well-studied example of a psychological adaptation that evolved to address the adaptive problem of sexual infidelity (Buss, 2000; 2018; Daly et al., 1982). Although jealousy is most typically thought of as only an emotion, it is actually an adaptation that includes many functional design features, such as sensitivity to cues of a partner's infidelity, sensitivity to contexts in which there is an increased likelihood of infidelity, and other contextual factors, such as mate value discrepancies and the presence of mate poachers (Buss, 2011). The emotion of sexual jealousy can be extraordinarily powerful, intruding on people's thoughts and pushing them to run mental simulations of actions capable of ameliorating their bad feelings. By considering the enduring and transient contextual factors impacting the problem, a behavioral solution is chosen to prevent or address the infidelity. Although many of these factors have been identified, more research is needed to understand how they interact to produce specific behavioral responses.

Victim Psychology

The predictable, recurrent use of violence and other cost-inflicting strategies in response to certain adaptive problem contexts would have created selection pressure on victims to avoid or minimize the physical and reputational costs of

being violently attacked. Threats of violence are only effective in altering victims' behavior because victims are motivated to avoid the greater costs of actual violence (Campbell, 1999; Cross & Campbell, 2011; Duntley, 2015). For example, women may cut off relationships with friends, distance themselves from family, and capitulate to sexual coercion to avoid the potentially greater costs of being injured by their mates. Women's use of aggression to defend themselves from their partner's violence is another proposed evolved victim defense (Duntley, 2015).

Children are women's most valuable fitness resources. Threats to their children are comparable or even direr than threats to women themselves, selecting for the umbrella of women's victim adaptations to also cover their children. Women's children from ex-mates are at greater risk because they do not directly enhance, and likely decrease, their stepfathers' fitness (Daly & Wilson, 1988). Stepchildren can also decrease their stepfather's fitness by preventing their mothers from having as many children in the future, or diverting some of her maternal investment from offspring she shares with her new mate. As a result of the greater risk of violence to children when a stepparent is in the home, women's adaptations to defend her children from victimization may be more sensitive and reactive in a stepfather's presence (Buss & Duntley, 2011).

Adaptations that produce violence and adaptations to defend against violence in mateships are hypothesized to be the result of coevolutionary arms races (Buss & Duntley, 2011; Duntley, 2015). A violent strategy that was ancestrally effective would have decreased victims' fitness, selecting for more effective defenses. More effective defenses would have decreased perpetrators' fitness, selecting for more effective use of violence or other, nonviolent tactics. Knowledge of the coevolutionary processes that shaped adaptations that produce violence and adaptations that defend against it has important implications for understanding patterns of violence and victimization in the variety of adaptive problem contexts in which it occurs. Further research will move us closer to minimizing the costs and perhaps someday eliminating mating violence.

The Value of an Evolutionary Approach to Mate Violence

Complete romantic harmony is the ideal of mateships but is rarely achieved. Although there is overlap in the fitness interests of men and women in long-term relationships, their fitness optima differ. Conflict between the sexes over the allocation of reproductively relevant resources is common and pervasive in long-term relationships. To pull their respective fitness optima in their favor, men and women have evolved a spectrum of tactics that range from delivering benefits to

inflicting costs. Cost-inflicting tactics range from relatively mild forms such as repeated phone calls and requests to meet to extreme forms such as violent assaults. An evolutionary perspective recognizes many cost-inflicting tactics in mateships as the output of adaptations that evolved to address specific, ancestrally recurrent adaptive problems, which include mate poachers, sexual infidelity, genetic cuckoldry, conflict over resource allocations, mate value discrepancies, relationship termination, and mate reacquisition (Buss, 2021).

Although evidence is supportive of evolutionary hypotheses about many of these adaptive problem domains, we are only beginning to explore others. For example, we do not know the precise combination of contextual factors that motivate violence or those that activate victim defenses. But an evolutionary approach provides a rich set of tools to investigate them. Additionally, an evolutionary approach to understanding mating violence complements other perspectives (see Frieze, 2005; Miller, 2012; Shorey et al., 2008). For example, irrational persistence and violence in ex-mate stalkers explained by relationship goal pursuit theory (Davis et al., 2012) can also be understood in terms of the adaptive problems of mate value discrepancies and mate reacquisition. If a woman ends the relationship with her partner because she is higher in mate value, it will be difficult for the man she rejected to attract a different mate who is as attractive as she is, since people prefer to couple with those who have mate values similar to their own. The man's best chance may be to try to regain the relationship with the mate who left him. Since he was already successful at attracting his ex-mate once, he would likely have a better chance getting her back than attracting a new mate of similar value. The man's seemingly irrational persistence may have paid off for ancestral men who faced the same problem, giving them better mating opportunities than they could have otherwise obtained. Rather than replacing relationship goal pursuit theory, the addition of evolutionary hypotheses provides additional levels of explanation and a clearer understanding of the irrationally persistent and violent stalking of ex-mates.

The coevolutionary approach to mating violence presented here represents an early step that may help guide future research. Understanding the evolutionary origins of violence between mates is essential because ancestrally recurrent problems are at the root of mating conflicts that predictably produce partner aggression. An evolutionary perspective provides a powerful tool for carving the nature of mate violence at its joints, supplies essential guidance about what to investigate, and offers a metatheoretical structure for uniting all research on violent mates.

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CHAPTER
25

The Dark Triad Traits and Mating Psychology

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Abstract

A common misconception among researchers and laypeople is that socially undesirable traits (e.g., aggressiveness) cannot be evolutionarily important and instead must be pathologies. The assumption is that if we—as a society—disapprove of certain behaviors, attitudes, and cognitions, these "pathologies" are then likely to be discouraged, minimized, and eradicated. Further, it is assumed that these undesirable features cannot simultaneously have some desirable or evolutionarily important functions. One potential example of this is found in the research on the Dark Triad traits of psychopathy, Machiavellianism, and narcissism. These traits have a history of research and social perceptions that label them undesirable in etiology, function, and sequelae. In this chapter, we review the evidence and logic of how these traits might be pseudopathologies, or adaptations (i.e., historically increased reproductive fitness of their bearers), while still recognizing that having these traits may come with associated costs to the individual and those around them. We present the argument for these traits as "fast" life history strategies and then detail the mating psychology linked to them. We close with a consideration of conceptual and methodological limitations and suggestions for future research to guide and encourage researchers.

Key Words: Dark Triad, psychopathy, Machiavellianism, narcissism, life history strategy

Psychology has a long history research on "darker" or undesirable aspects of

personality. The most common viewpoint of these traits is that they are pathologies and should be managed, reduced, and eradicated, if possible. Recently much work on personality psychology has turned to these topics in subclinical populations in the form of the Dark Triad of personality. Psychopathy, narcissism, and Machiavellianism (Furnham et al., 2013) have long traditions in clinical, social, and personality psychology suggesting they are traits linked to selfishness, agency, impulsivity, criminality, and a variety of other undesirable outcomes. It is no surprise then that the predominant paradigm to study these traits assumes they are pathologies for the person and society. However, over recent years an alternative way of seeing these traits has been gaining momentum. The approach attempts to understand why, for example, these traits might enable someone to engage in a short-term mating style (Jonason et al., 2009, 2011) and how these traits may be linked to reproductive success in men (Carter et al., 2018) and reproductive costs in women (Jonason & Lavertu, 2017).

Researchers adopting this alternative view of the dark side of personality overwhelming adopt a midlevel theory about how organisms deal with survival and reproductive challenges, life history theory (Wilson, 1975). Life history theory was originally used to describe differences between species in terms of how organisms allocate finite resources in time and metabolic energy to the two most fundamental Darwinian tasks of survival (i.e., somatic) and reproduction (i.e., mating). Life history theory is an interactionist framework that describes how organisms, situated in a particular socioecology (e.g., harsh or unpredictable), solve the four F's of life: feeding, fighting, fleeing, and finding mates. Selective pressures have shaped species-level characteristics by pruning (but not wholly eliminating) variation in life history strategies that did not result in reproductive success. How ancestral forms solved Darwinian challenges can be seen in species-level differences today. Organisms that trade off mating for survival are called *slow* or *K*-selected life history strategists and have (relatively) long lives, long developmental periods, a high level of cognitive sophistication, and a small number of offspring in their lifetime (e.g., *Pan troglodytes* [common chimpanzee] and *Loxodonta africana* [African elephant]). In contrast, organisms that trade off survival for mating are called *fast* or *r*-selected life history strategists and have (relatively) short lives, mature quickly, are less cognitively sophisticated, and have a large number of offspring in their lifetime (e.g., *Rattus rattus* [Black rat] and *Oryctolagus cuniculus* [European rabbit]).

Even though species can be described in terms of how they solve these adaptive tasks, such descriptions should not be taken as evidence of some predestined, perfect fit between organisms and their environments. Conflicts

occur when an organism's ancestral adaptations mismatch their current living conditions. For example, bears as a taxon are opportunistic omnivores with a heavy focus on animal protein (e.g., salmon and seals). As a result, ursine have a generalist digestive system that tends to have a short intestinal system (short intestines are also common in carnivores). However, one bear species found itself living in an environment that could only reliably afford it a rather low value and hard-to-process food—bamboo. Short intestines are the death knell for a ruminator (bovines are ruminators) because they cannot extract the resources needed and, in the end, actually defecate out much of the limited resources possible in low value foods like grasses of which bamboo is one. The giant panda bear (*Ailuropoda melanoleuca*) found itself an obligatory ruminator causing conflicts in how they trade off mating and survival efforts. They spend most of their days (≈ 14 hours/day) eating bamboo (i.e., 99 percent of their diet) leading to a deleteriously limited time to engage in mating. Nevertheless, it is likely that within the species, there are individual differences in processing food and behavioral choices that may lead to differential reproductive success within the species with certain pandas outperforming others. The same can be said of humans who are, a species, slow life history strategists but, as individuals, differ to the degree that they fit the species-level pattern with some opting for potential alternative life history strategies.

Some behavioral syndromes facilitate more survival and reproduction than others and members of the species that have the "optimal" behavioral syndromes will have outcompeted others in evolutionary challenges. What a biologist calls within-species "behavioral syndromes," psychologists call "personality traits" or "individual differences." These psychological differences between members of the same species allow them to (1) occupy different niches and (2) calibrate their approaches to solving adaptive challenges in response to local contingencies. For example, those characterized by psychopathy and narcissism appear to have a bias toward wanting to live in cities, where they can find the mating opportunities they want while minimizing their exposure for getting caught for engaging in a "cheater strategy" (Jonason, 2018). In contrast, those living in more competitive environments like Turkey are better characterized by narcissism than those who live in less competitive places like Australia (Jonason et al., 2019); being more agentic should serve adaptive goals in competitive spaces.

Whereas most research on evolutionary personality psychology (and personality writ large) tends to focus on socially desirable manifestations of personality like the Big Five traits or empathy, socially undesirable traits could be adaptive, despite the social and personal costs they impose, if the net benefits

outweigh the net costs. Over evolutionary time, the traits can then be maintained in the species' repertoire as opposed to being actively selected against. A common mistake among laypeople, critics of evolutionary approaches to human behavior, and amateur evolutionary psychologists is that traits that are socially undesirable cannot be adaptations. This misunderstanding comes from several sources. First, people tend to construe the colloquial usage of the word "adaptive" to be psychosocially beneficial (Jonason et al., 2020b). When the same (and related) term (i.e., "adaptation") is used in its technical, Darwinian sense, it is confined to its relationship with reproductive fitness. Second, traits that are considered socially undesirable are often vilified because of the externalities they impose on others, but this says nothing about whether it is beneficial to the person with the trait (Jonason et al., 2015). Third, socially undesirable traits tend to lead people to engage in agentic behaviors that make them stand out from the crowd (Jonason et al., 2020a) which violates people's groupish leanings. In the rest of this chapter, we review one set of socially undesirable traits—the aforementioned Dark Triad traits—in relation to mating psychology with a focus on understanding the costs and benefits and the context specificity of these traits as they operate in facilitating reproductive outcomes.

The Dark Triad traits

Researchers have grown considerably interested in three related, adverse personality traits, known as the Dark Triad, composed of narcissism, Machiavellianism, and psychopathy. Narcissism is associated with a sense of grandiosity, egotism, self-orientation, and lack of empathy (Turner & Webster, 2018), Machiavellianism is associated with manipulative behavior, self-interest, exploitation of others, and a ruthless lack of morality (Jones, 2016), and psychopathy is associated with reckless, cruel, and callous attitudes; antisocial selfish behavior; lack of empathy; and a lack of remorse (Cale & Lilienfeld, 2002). All three traits have long, relatively independent research traditions that we cannot hope to cover here (see Zeigler-Hill & Marcus, 2016). Instead, we briefly try to make the case that these traits might reflect *fast* life history strategies before turning to the topic of mating psychology.

A considerable case has been made for the evidence consistent with the hypothesis that the Dark Triad traits (typically in their subclinical manifestation) are fast life history strategies (see Koehn et al., 2019). The term "fast" is a descriptive term that simplifies a more complicated reality. "Fast" is not about speed necessarily (especially in the realm of psychology) but, more accurately, about self-interested as opposed to other-interested social strategies when

applied to psychology. For example, species that are considered “slow” tend to be more communal and teach offspring (e.g., elephants) whereas “fast” species may live in groups but not in a cooperative fashion (e.g., mice). This paradigm allows researchers to ask unique questions and account for apparently maladaptive patterns associated with these traits. For example, the classic interpretation of the link between psychopathy and limited empathy is that the latter is a manifestation of the pathological nature of the former. However, seen through an evolutionary lens, there may be a less biased way of seeing this pattern. Instead of assuming that psychopathy is a pathology, perhaps it is a “predator” adaptation (Mealey, 1995). If so, (1) men should be lower on empathy and higher on psychopathy, (2) psychopathy should be linked to limited empathy because empathy would interfere with predation, and (3) the limited empathy characteristic of those high in psychopathy should be strongest in men compared to women. Indeed, those predictions have received some support (Jonason et al., 2013b). Therefore, although traditionally considered pathologies (Kowalski, 2001), these traits might be pseudopathologies (Crawford & Anderson, 1989) whereby they benefit the individual at the expense of the group and even the individual themselves.

Taking our lead from work in evolutionary biology, researchers have examined an array of indicators and outcomes that are consistent with the hypothesis that the Dark Triad traits may enable a fast life history strategy. That is, they are part of the psychological system that helps people prioritize their own needs at the costs of others even when doing so might be dangerous and even damaging to them (Jonason & Zeigler-Hill, 2018). For example, men more than women are characterized by these traits around the world (Jonason et al., 2017a; Jonason et al., 2013a). Because men suffer fewer fitness costs associated with engaging in a fast approach to life, the phenotype responsible for creating dispositions that lead to the related behaviors should be and are less common in women. That is, natural selection would have operated differently in each sex based on the asymmetries in costs and benefits over ancestral time. Evidence also suggests the Dark Triad traits facilitate a short-term (Jonason et al., 2009) and exploitive (Jonason et al., 2017b) mating strategy, limited family- or friendship-based motivations (Jonason & Zeigler-Hill, 2018), limited existential values (Jonason et al., 2018), a tendency to prioritize immediate outcomes over delayed ones (Jonason, Koeing et al., 2010), a competitive approach to social interactions (Jonason et al., 2020c), and impulsivity (Jones & Paulhus, 2011). All these correlated traits and behaviors are likely to facilitate a fast life history strategy, not bonding individuals to others but, instead, extracting resources from others and the world for their own, often short-term, benefits. The way these

traits manifest in intimate relationships will be discussed next in greater detail given the centrality of these relationships in affording people with (potential) reproductive fitness.

Mating Psychology and the Dark Triad traits

One of the most fundamental contributions of this research has been the exploration of individual differences in mating psychology as a function of the temporal duration and level of investment of a relationship (Buss & Schmitt, 1993; Schmitt, 2016; Schmitt et al., 2001). In the short-term context (e.g., one-night stands), men tend to invest less than women do (e.g., no risk in getting pregnant) whereas in the long-term context (e.g., marriage), both sexes invest similar amounts of time and resources to the relationship and the offspring (Geary, 2016). Given these divergent contexts and competing interests, mating is a complex human motive that requires a great deal of effort, psychological resources, time, trade-offs, and compromises (Buss, 2008). Different people solve these problems in different ways (Buss, 2016). In the following sections, we detail how those characterized by the Dark Triad traits may solve the problems present in short-term and long-term contexts along with their specific mate preferences.

The Dark Triad traits and Short-Term Mating

Individuals high on the Dark Triad traits manifest a series of attitudes, cognitions, emotions, and behaviors that may be described as facilitating mechanisms of short-term mating. We can see that individuals with high scores on the Dark Triad traits (1) offer great importance to sex (Baughman et al., 2014), (2) prefer certain types of romantic relationships (e.g., one-night stands), and situations where they can facilitate their short-term mating orientation (Jonason et al., 2012), (3) are unfaithful in their relationships and engage in mate poaching (Jones & Weiser, 2014), (4) use aggression in the mating context, and are perceived by others as potential sexual aggressors (Blinkhorn et al., 2015; Pavlovic et al., 2019), and (5) offer great importance to their physical appearance (Chegeni & Atari, 2017). As such, personality traits—that are to a great extent reflections of fast life history strategies (Figueredo et al., 2006)—may reflect how people high on the Dark Triad traits facilitate their short-term mating orientation and how they extract reproductive benefits. Fast or slow life history strategies may simply be lexical summaries that capture variation in the functioning and sensitivity of a wide variety of species-typical adaptions

(Lukaszewski et al., 2020). We detail these characteristics and mechanisms in the following paragraphs.

The link between the Dark Triad traits and interest in casual sex may be explained by the fact that the traits reflect an orientation to seek stimulation and to take advantage of immediate sexual opportunities (Jonason et al., 2012). Also, those high on the Dark Triad traits lower their standards for possible mates, and interest in sex (Baughman et al., 2014) may be a motivational force that encourages individuals to lower their standards when deciding with whom to engage in sexual activity (Jonason et al., 2011). In this regard, people high on the Dark Triad traits are characterized by a higher mating effort (Egan & McCorkindale, 2007; Westhead & Egan, 2015). Moreover, people high on Machiavellianism and psychopathy manifest high intrasexual competition (Lyons et al., 2019a), and those high on psychopathy and narcissism report a high-quality sex life (e.g., lower negative emotions in the sexual context; Pilch & Smolorz, 2019) and19b a high frequency of sexual dreams (Lyons et al., 2019b). In a similar fashion, individuals high on psychopathy report limited sexual disgust (Burtăverde et al., 2021), which should facilitate engaging in more casual sex (Al-Shawaf et al., 2015).

Further, people with high scores on the Dark Triad traits are attracted by contexts and environments (e.g., city living; Jonason, 2018) that favor their short-term mating orientation and prefer certain types of romantic relationships (Jonason et al., 2012). They do so by using strategies and tactics that enable them to avoid entangling commitments, and by using strategies such as minimizing escalation to a long-term relationship, keeping the relationship sexual in nature, thereby avoiding contact and intimacy (Jonason & Buss, 2012). This is sustained by further evidence on the type of relationship people with high scores on the Dark Triad traits prefer. Individuals high on narcissism prefer one-night stands and friends-with-benefits relationships, whereas individuals with high scores on psychopathy prefer booty-call relationships (Jonason et al., 2012; Koladich & Atkinson, 2016). Also, individuals high on psychopathy and Machiavellianism are more likely to use the dating application Tinder for casual sex (Jonason & Bulyk, 2019; Timmermans et al., 2018) and the Dark Triad traits are associated with sexting (Clancy et al., 2019; March & Wagstaff, 2017) which also may be manifestations of the short-term mating orientation of those high in the Dark Triad traits.

The Dark Triad traits are associated with infidelity in both men and women (Alavi et al., 2018; Brewer & Abell, 2015; Jones & Weiser, 2014). Individuals high on the Dark Triad traits engage in infidelity because they are low in empathy (Jonason et al., 2013b) and may be unconcerned with hurting others.

This view is supported by compelling evidence. Psychopathy and Machiavellianism are predictors of infidelity (Jones & Weiser, 2014). Women high on the Dark Triad traits report prior experiences of infidelity, intentions to engage in infidelity, and perceived susceptibility to a partner's infidelity (Brewer & Abell, 2015). The relationship between narcissism and psychopathy, on the one hand, and intentions to infidelity on the other hand, is moderated by relationship experience (Alavi et al., 2018). Individuals high on narcissism intended to be unfaithful if they were in a long-term romantic relationship, while those high on psychopathy intended to be unfaithful if they were in a short-term relationship. There are some possible explanations why people high on the Dark Triad traits are successful in being unfaithful and continuing the relationship. Individuals with high scores on the Dark Triad traits engage in sexual deception (e.g., blatant lying, self-serving deception, and avoiding confrontation; Brewer et al., 2019). Also, the fact that individuals high on the Dark Triad traits are unfaithful may be explained by the fact that the Dark Triad traits play an important role in engaging in extra-pair relationships and risk tolerance regarding the possibility of detection (Adams et al., 2014). Moreover, individuals high on the Dark Triad traits care little about keeping their partners, as they manifest limited mate retention tactics and are more likely and willing to steal or "poach" mates from others (Jonason et al., 2010). These findings suggest that individuals high in the Dark Triad traits use sexual deception to facilitate their short-term mating orientation.

Individuals high on the Dark Triad traits use sexual aggression in their romantic relationships (Lyons et al., 2020). This may be because dispositions that facilitate rape may have evolved (Barnes et al., 2013), because there may be some advantages related to the reproductive success of these dispositions—sexual coercion is linked with more offspring in our closest living relatives, chimpanzee (*Pan troglodytes*; Feldblum et al., 2014). Important evidence supports this view. Narcissistic men and women engage in sexually coercive tactics (Blinkhorn et al., 2015; Lyons et al., 2020). Also, people have the tendency to perceive that there is a high probability of being raped by individuals high on the Dark Triad traits (Pavlovic et al., 2019). Moreover, men high on the Dark Triad traits have more rape-enabling attitudes (Jonason et al., 2017b). Partner-directed violence is linked with cost-inflicting mate retention tactics such as vigilance, monopolization of mate's time, emotional manipulation, direct guarding, and intersexual negative inducements (Shackelford et al., 2005).

People high on the Dark Triad traits, especially those with high scores on narcissism and psychopathy, are perceived by others as attractive (Holtzman &

Strube, 2013). This perception is explained by the fact that people high on the Dark Triad traits adorn their physical appearance, a strategy that may facilitate their mating success because it enhances their chances of attracting new mates (Chegeni & Atari, 2017). Also, individuals high on narcissism make a good first impression, and are perceived as popular and charismatic (Back et al., 2010). In an experimental design based on a scenario setting (where fictitious opposite-sex target person's traits were described), people perceived others who were high on narcissism as desirable and attractive (Rauthmann & Kolar, 2013). This means that individuals high on narcissism enhance their physical attractiveness to make a good first impression, which may be an effective strategy to succeed in a short-term mating context for both sexes.

The Dark Triad traits and Long-Term Mating

The way individuals high on the Dark Triad traits behave in long-term romantic relationships has been studied to a lesser extent given the compelling evidence that individuals high on the Dark Triad traits have a short-term mating strategy (Jones & de Roos, 2017; Valentova et al., 2020). However, this does not mean that these individuals do not engage in long-term relationships (Brewer & Abell, 2015; He et al., 2018; Smith et al., 2014; Tsoukas & March, 2018). The reason they engage in long-term relationships may be to extract reproductive benefits related to long-term mating (e.g., the relative but not absolute improvement in offspring survival in the case of short term-mating compared to long-term mating; Geary, 2016). In the case of individuals high on narcissism, they may prefer long-term relationships to maintain access to positive attention, self-esteem, and sexual resources (Tsoukas & March, 2018). Individuals high on the Dark Triad traits who engage in long-term relationships (1) have poor relational skills and low relationship satisfaction (He et al., 2018), (2) use cost-inflicting mate retention tactics (Jonason et al., 2010), and (3) engage in assortative mating (Jonason et al., 2015).

Individuals high on the Dark Triad traits have poor relationship skills in long-term romantic relationships (He et al., 2018). This may be because they lack empathy (Jonason & Krause, 2013), and they may be unconcerned with the needs and feelings of their partner. In dyadic settings, women's level of the Dark Triad traits predicts low levels of men's commitment (Smith et al., 2014). In research on couples, the level of psychopathy rated by the partner, led to marital instability perceived by both partners, a key feature of this association being interpersonal rejection (He et al., 2018). Moreover, people characterized by secondary psychopathy (i.e., antisocial, reckless, impulsive behavior; Levenson

et al., 1995) were also characterized by attachment anxiety, while those high on Machiavellianism, primary psychopathy (i.e., manipulative, selfish, lack of empathy; Newman et al., 2005), and secondary psychopathy were characterized by attachment avoidance (Brewer et al., 2018). The idea that individuals high on the Dark Triad traits have poor relational skills in long-term mating relationship is sustained by the fact that these individuals are characterized by specific love styles like ludus (i.e., game-playing; Jonason & Kavanagh, 2010). Being characterized by such love styles may allow them to keep others at an emotional distance to maintain their short-term mating style. As such, individuals with high levels of the Dark Triad traits, because of their limited empathy, lack interpersonal skills in terms of intimacy and closure, which are vital for the functioning of long-term relationships (Inansi et al., 2015).

Further, individuals high on the Dark Triad traits that engage in long-term mating use cost-inflicting mate retention tactics (Jonason et al., 2010). This may be because they know that, in general, they are perceived by others as undesirable (even though individuals high on narcissism may not believe that), and it may be hard for them to find other mates if they lose their current partner. Important evidence supports this view. For example, individuals with high scores on the Dark Triad traits manifest break-up distress (Moroz et al., 2018). Also, individuals high on the Dark Triad traits are more likely to take revenge against a romantic partner (Rasmussen & Boon, 2014). The cost-inflicting and negative mate-retention tactics used by individuals high on the Dark Triad traits were identified in dyadic research that investigated the link between the Dark Triad traits and aggression in a long-term romantic (Webster et al., 2016). Moreover, in research on couples, self-reported effects of the Dark Triad traits on mate-retention behaviors were stronger in men, while the levels of the Dark Triad traits reported by men (self-assessed) led to women's mate-retention behaviors (Kardum et al., 2019). Also, men and women high on the Dark Triad traits engage in a wide variety of romantic jealousy manifestations (Barelds et al., 2017; Burtăverde et al., 2021; Chin et al., 2017), these manifestation being stronger if those high on Machiavellianism perceive themselves as having low mate value (Burtăverde et al., 2020). It seems that the relationship between the Dark Triad traits and mate-retention behaviors tend to be universal and cross-culturally valid, taking into account the evidence that comes from non-Western societies (Chegeni et al., 2018; Kardum et al., 2019). However, it should be noted that some ecological factors may be important in the case of the link between the Dark Triad traits and mate retention as Iranian men scored higher on domains of mate retention (Chegeni et al., 2018).

Besides cost-inflicting mate-retention behaviors, it seems that individuals

high on the Dark Triad traits use sex-specific-mate retention tactics like faking orgasm. Women high on Machiavellianism pretend more frequently (Brewer et al., 2016), which may represent a sexual mate-retention tactic that helps women maintain their long-term relationship and the benefits associated with it (e.g., being sure that the partner invests his resources in the relationship). The Dark Triad traits may be linked to selfish, hedonistic reasons (e.g., avoiding boredom) for faking orgasm (Jonason, 2019).

Individuals high on the Dark Triad traits prefer mates who are like them (i.e., positive assortative mating; Blanchard et al., 2016; Jonason et al., 2015; Kardum et al., 2017). This may happen because it would be easier for individuals high on the Dark Triad traits to pursue their mating goals (casual sex, lack of empathy, and a Ludus love style, etc.) if the partner resembles them in terms of personality (and implicitly in goals and mating strategies). Men high on the Dark Triad traits may prefer women who are also high on the Dark Triad traits for short-term mating, because those women would be more willing to satisfy men's need for casual sex and sexual variety. For long-term relationships, men with high scores on the Dark Triad traits might prefer women oriented to long-term mating on which they can be unfaithful, but at the same time, they can have the benefits of a long-term romantic relationship.

Women who are high in psychopathy perceive men with high levels of the Dark Triad traits as physically attractive and desirable for one-night stands, and as a potential husband as well, while men who were high on psychopathy were likewise attracted to psychopathy in potential mothers. In addition, individuals high on primary and secondary psychopathy perceive similar individuals as attractive for both short- and long-term relationships (Blanchard et al., 2016). Regarding the effects of similarity on the Dark Triad traits on the quality of the relationship in dating couples, similarity in narcissism was related to high perceived relationship quality in both sexes (Kardum et al., 2018).

Limitations, Future Directions, and Conclusions

Despite the burgeoning nature of the research on the Dark Triad in general (Furnham et al., 2013; Koehn et al., 2019) and in relation to mating specifically, there are several limitations that qualify our discussion here and encourage future research. First, it is unclear if the Dark Triad traits are sufficient to cover so-called darker aspects of personality. For example, there are campaigns to also include sadism (Buckels et al., 2013) and spitefulness (Marcus et al., 2014). These traits may be interesting, but it is unclear whether they add much to our understanding of various motives and attitudes (Jonason & Zeigler-Hill, 2018;

Jonason et al., 2017d) and even less clear if they add more to our understanding of romantic and sexual psychology. Without sufficient evidence, it may be more parsimonious to treat sadism and spitefulness as a downstream manifestation of psychopathy making it more a mechanism that could link psychopathy to particular outcomes like cyberstalking. However, a corollary concern is that it is unclear whether Machiavellianism and psychopathy are also redundant. These traits are also highly correlated, maybe even multicollinear (Bertl et al., 2017; Miller et al., 2016; Trahair et al., 2020); multicollinearity might be created by a higher-order *D* factor running through several "dark" traits (Moshagen et al., 2020). Unlike sadism, however, there is more evidence that Machiavellianism is linked to different outcomes than psychopathy, such as race-based prejudice (Jonason et al., 2020c), suggesting that it is not fully redundant to psychopathy (see Jones, 2016).

Second, although the general area of research is starting to incorporate samples from around the world (Jonason et al., 2017a; Jonason et al., 2013a; Jonason et al., 2019; Jonason et al., 2020d), research on the romantic and sexual psychologies of people is markedly characterized as WEIRD (i.e., Western, educated, industrialized, rich, and democratic; Henrich et al., 2010). When it is not, it tends to be monocultural in nature as opposed to attempting to understand cross-national variance in how the Dark Triad traits relate to mating motives. While it is unclear how culture might influence the mating psychology linked to the Dark Triad traits, given the centrality of ecological harshness/unpredictability in life history models of personality, such an endeavor is likely not only warranted but will be informative.

Third, much of the evolutionary work on the Dark Triad traits hinges on the assumption that they act as adaptations for exploitation. However, there is limited research on their adaptive benefits. One important consideration is whether the traits lead to greater reproductive success. There is limited evidence linking Dark Triad traits to the number sex partners people have (Jonason et al., 2009) and number of offspring (Carter et al., 2018). If we are to trust the life history arguments that these traits are adaptations for exploitation, more work is called for to understand the functional utility and adaptive features of the Dark Triad traits. That said, there is evidence (Wroblewski et al., 2009) in chimpanzees (*Pan troglodytes schweinfurthii*) from Gombe that a former resident-bully (i.e., Frodo) had the most offspring, just eking out his more coalitionary-building brother (i.e., Freud). Workers at this reserve apparently took to calling Frodo their resident "bad boy" (Wroblewski, 2009, personal communication).

Fourth, there are several methodological limitations, much of which are a

function of limited funding in both Dark Triad research and relationship research. Most studies have relatively small sample sizes by modern standards, rely on cross-sectional data, rarely adopt person × situation interaction tests, and exclusively rely on self-reported personality. Although self-report methods are quite hard to escape when it comes to the measurement of personality and individual differences, the other issues are less challenging. However, taking into consideration modern concerns of replication and sample size/power, experimental studies (and cross-national studies) need to have an exceedingly large sample size to ensure sufficient power for all pairwise comparisons (but see Jonason et al., 2020d).

Fifth, beyond these methodological concerns, there are conceptual concerns. For example, it is unclear whether the traits are adaptions themselves or simply lexical and behavioral summaries of the downstream results of the adaptations (Lukaszewski et al., 2020. This work highlights socioanalytic approaches to the Dark Triad traits in that they are downstream behavioral syndromes of upstream adaptations like biased ways of seeing social situations (Jonason & Sherman, 2020; Zajenkowski et al., 2020) along with other more basic units of psychology (e.g., motivation and affective systems). According to this view, the correlations between the Dark Triad traits and many of the outcomes we have suggested above are likely spurious, and the Dark Triad traits are not actually adaptations themselves but, instead, aggregate manifestations of the adaptations that are more easily observed in the fashion of logical positivism's view of phenomena like black holes. For example, promiscuity and psychopathy may merely be linked because of their shared link to more fundamental individual differences than what are commonly referred to as personality traits today. Another conceptual concern stems from whether researchers can apply life history thinking within species, especially, to humans. This concern relies on the idea that the processes that genetically fit species to their environments (e.g., natural selection) are different from the processes (i.e., correlational selection, physical linkage, and pleiotropy) that fit the individuals of a certain species to their environments (called developmental plasticity; Zietsch & Sidari, 2019). Nevertheless, recent evidence has provided a major advance in understanding the socioecological conditions within countries linked to the Dark Triad traits and sex differences therein, evidence consistent with life history predictions (Jonason et al., 2020d).

In closing, we assert that life history and evolutionary approaches to the Dark Triad traits (along with other dark traits) may be a fruitful avenue of research. We have only summarized work in the intimate relationship domain, but the approach may also be useful in other domains like organizational psychology

(e.g., Jonason et al., 2014), intergroup relations (e.g., Żemojtel-Piotrowska et al., 2020), and health psychology (e.g., Nowak et al., 2020). While we appreciate the traditional approaches to these traits which are geared to the detection of these traits to help others and to protect ourselves from the externalities that may be imposed by people characterized by these traits, a more complete picture can be afforded with an examination of the function of these traits in people's lives. Such an examination may reveal why these traits exist and persist in populations.

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CHAPTER
26

Sexual Harassment

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Abstract

Sexual harassment is widely recognized as a serious problem in the workplace, and a nuanced understanding of it is a necessary precondition to effective management. Much of the social science literature contends that sexual harassment is "not about sex but about power." An evolutionary perspective, though acknowledging the link between sex and power, suggests that the causal implication of social scientists is often backward and that much behavior that is labeled sexual harassment reflects the different sexual strategies of males and females. It is less that men use sex to obtain power over women than it is that they use power to obtain sex, as they have throughout our evolutionary history. The fact that harassers tend to prefer young, attractive targets—that is, those who possess traits that are desirable in a consensual partner—reinforces the view that they are acting on sexual motivations. An understanding of the different sexual psychologies of males and females also sheds light on the question whether a reasonable-person standard or a reasonable-woman standard should be used to assess whether an environment is a hostile one. Men and women often perceive situations differently because of their evolved psychologies, so that an androgynous reasonable-person standard makes little sense. An evolutionary perspective, with its more realistic explanation of sexual harassment than its purely sociological competitors, is more likely to lead to effective mechanisms to combat it.

Key Words: sexual harassment, reasonable person, sex versus power, mating motivations, sexual strategies, evolution, workplace

The picture of women and men working side by side, doing the same work and competing for positions in the same status hierarchies now seems quite natural and even normative. Yet it must be recognized that this is an evolutionarily novel situation, far different from the environment in which our distant ancestors evolved, leading to an "evolutionary mismatch" (Li et al., 2018). It was expected by many that repudiation of the universal sexual division of labor would lead men and women to act identically in the workplace, be proportionately represented in all occupations, and earn the same amount of money, but psychological sex differences have intervened, resulting in phenomena such as the glass ceiling, the gender gap in compensation, and de facto occupational segregation (Browne, 2002).

Sexual conflict is ubiquitous in human societies (Buss, 2017), and as the workplace has become increasingly sexually integrated, opportunities for sexual conflict have proliferated (Browne, 1997, 2002, 2006). When sexual conflict occurs, it is often in the form of sexual harassment. Although sexual harassment is commonly considered primarily a workplace phenomenon, it can occur virtually anywhere that the sexes interact, be it in schools (Kennair & Bendixen, 2012), in bars (Graham et al., 2017), on the street (Shah, 2016), or over the internet (Ritter, 2014). Workplace sexual harassment has been called "one of the most damaging and ubiquitous barriers to career success and satisfaction for women" (Willness et al., 2007, pp. 73–74), but estimates of its incidence vary widely (Gutek et al., 2004). The US Equal Employment Opportunity Commission (EEOC) estimates that 25 percent to 85 percent of women have been victims of workplace harassment (EEOC, 2016), a range whose breadth does not inspire confidence in the metric.

This chapter examines two issues that have figured prominently in the sexual harassment literature and suggests that incorporating the insights of evolutionary psychology provides a more robust understanding than the purely sociocultural explanation. The first issue involves the claim that sexual harassment is not "about sex" but "about power." According to this view, when a male supervisor makes sexual demands on a woman, he is using sex to obtain or retain power over the woman.[1] Although such claims may appeal to those with an exclusively sociological orientation, to an evolutionist the claim that sexual behavior is commonly not "about sex" seems farfetched given the centrality of sex to reproductive success. Sometimes (in fact, mostly) a cigar is just a cigar, and when men pursue sex, it is likely because they want sex.

The second issue is how to assess whether a hostile environment exists. Should one consider it through the eyes of a "reasonable person" or a "reasonable woman"? An evolutionary perspective—which reflects an

understanding of the differing selective pressures faced by the two sexes and the resultant differences in sexual psychologies—suggests that in matters of sex, there are "reasonable men" and "reasonable woman" but no such thing as a "reasonable androgyne" (Tiger, 1997, p. 79).

What Is Sexual Harassment?

Sexual harassment is considered a form of sex discrimination under the laws of the United States (Browne, 1997), the United Kingdom (Clarke, 2007), and the European Union (Numhauser-Henning & Laulom, 2012). The principal US law governing sex discrimination in the workplace—Title VII of the Civil Rights Act of 1964—does not even mention the term "sexual harassment." Instead, courts have held that sexual harassment violates the statute's general prohibition against discrimination "because of sex" (*Meritor Savings Bank*, 1986).

Although legal definitions are not the focus here, a brief description of legal doctrines may provide a useful perspective. The law recognizes two distinct categories of sexual harassment (Back & Freeman, 2018). The first is "quid pro quo harassment," which entails a claim that an employee was required to submit to sexual advances as a condition of either obtaining a benefit (such as promotion) or avoiding a burden (such as being fired). The classic example is the threat, "Sleep with me or you're fired!," although less-explicit threats may also fit the definition (Dacus, 2006). Such conduct is "sex discrimination" if the demand would not have been made had the employee been of the other sex. If the offending supervisor imposes sexual demands on males and females alike, however, it is less obviously sex discrimination, and courts have had more trouble with the few such cases that have come their way (Bible, 2010).

The second form of harassment is "hostile environment" harassment, which consists of a work environment that is permeated with sexuality or "discriminatory intimidation, ridicule, and insult" (*Meritor Savings Bank*, 1986, p. 65). Not all such conduct is legally actionable, however, as the conduct must be "based on sex," be "unwelcome," and be "sufficiently severe or pervasive to alter the conditions of the victim's employment and create an abusive working environment." The "severe or pervasive" requirement is intended to preclude liability for isolated incidents or behaviors that are "merely offensive." Moreover, the plaintiff must show not only that *she* perceived the environment as abusive but that the reasonable person or reasonable woman (more about this distinction later) would have found it so as well (*Harris v. Forklift Systems*, 1993).

Hostile environment harassment consists of a wider range of behavior. Like

quid pro quo harassment, it may consist of sexual advances, but they need not be tied to a tangible employment action. Unlike quid pro quo harassment, which requires that the harasser be a supervisor since only they can threaten tangible employment consequences, sexual advances creating a hostile environment might also come from peers, subordinates, or even customers. As in quid pro quo cases, these advances are deemed sex discrimination because they occurred "because of" the target's sex. Other kinds of maltreatment, whether sexual or nonsexual, directed at a woman because of her sex also fit within a discrimination model. Yet other offensive conduct does not fit the model so well, such as a sexualized work atmosphere filled with provocative pictures, sexual jokes, or sexist comments. There may be no specific target of that conduct, but the complainant may argue that such environments are inherently more burdensome to women than to men.

Power vs. Sex

It is frequently said that sexual harassment is not "about sex" but "about power" (Bravo & Cassedy, 1992, p. 16; Dougherty & McCormack, 2017, p. 2137), echoing equivalent claims about the motivations of rapists (Palmer & Thornhill, 2003). This argument assumes that sexual harassment is a unitary phenomenon with a unitary cause. Thus, Berdahl (2007, p. 425) asks whether sexual harassment "is motivated by sexual desire or by sexist antipathy," as if it must be one or the other. Yet sexual assaults, nonsexual assaults, attempts to maintain a soured relationship, sexual insults, sexist or sexual jokes, sexual pictures or cartoons, repeated requests for dates, employee sabotage, and well-intentioned compliments might have a variety of causes. An evolutionary approach acknowledges a multiplicity of causes but suggests that mating motivations are often present.

The distinction between "approach-based" and "rejection-based" harassment is a productive one. The former consists of behaviors, such as unwanted sexual attention, that "tend to imply sexual attraction," while the latter may "imply a desire to humiliate, punish, or otherwise drive away the target" (Stockdale et al., 2004, p. 159). The former behaviors may be attempts to exploit short-term (or even long-term) mating opportunities, while the latter seems inconsistent with a mating motivation and may be motivated by a wish to derogate workplace or sexual rivals (Bendixen & Kennair, 2017). Other behavior, such as untargeted sexuality, is hard to categorize as either approach-based or rejection-based.

Harassment and Sexuality

Much sexual harassment appears to be sexually motivated. Quid pro quo harassment seems guided by a sexual purpose even if it is the harasser's power that makes such extortion possible. Less-transactional behavior, such as persistent requests for dates or other sexual advances by coworkers, often has similar motives.

An analysis of sexual harassment incorporating insights about mating better explains harassment than does a purely power-based sociological interpretation. Studd and Gattiker (1991) showed that the demographic profile of targets is largely what would be expected if harassers were employing short-term sexual strategies (Buss & Schmitt, 1993). The strongest prediction is that the harasser is male and the victim is female, since men are usually the sexual initiators in both long-term and short-term mating. Other predictions are that the target will be of reproductive age, physically attractive, and not involved in a serious long-term relationship (thus lacking a male protector and competitor for sexual attentions). They found these predictions to be largely satisfied, with the overwhelming proportion of victims being single, divorced, or separated women under the age of thirty-five. They concluded that the motivation of most men involved in coercive sex in the workplace was indeed sexual (although not romantic). Supporting the notion that harassers' motives are at least perceived to be sexual is the fact that in laboratory studies subjects are substantially more likely to find that sexual harassment occurred when the plaintiff is attractive (Madera et al., 2007).

Bourgeois and Perkins (2003) claimed to have "overwhelmingly refuted" the evolutionary-psychology perspective on sexual harassment. They focused on the assertion of Buss (1999, p. 319) that "the degree of chagrin that women experience after sexual advances … depends in part on the status of the harasser," with women being *less* upset by advances from higher-status men than lower-status men. Bourgeois and Perkins, in seeming contrast, found that women report imagining *greater* upset if someone higher in their organization persisted in asking them out despite repeated refusals than if the requests came from someone lower in rank. This finding, they asserted, supports the sociocultural explanation and refutes the evolutionary explanation.

Rather than refuting the evolutionary psychology account, the Bourgeois and Perkins results actually support it. Their scenarios, unlike the study Buss was referring to, critically placed the high-status man *above the woman in the organization*. Two well-documented findings are relevant here. The first is that women tend to prefer high-status men to low-status men (Buss & Schmitt, 1993); thus, all else being equal, they are likely to find advances by the former more welcome than advances by the latter. The second finding is that women are

strongly averse to sexual coercion (Thornhill & Palmer, 2000). Therefore, women will suffer more distress when the possibility of sexual coercion is high than when it is low. These findings yield two further predictions. First, women are likely to find advances by high-status men more welcome than advances by low-status men in their own organizations; that is, they would be expected to prefer advances from a corporate executive to those from a mailroom clerk. Second, if the advances are *unwelcome*, women are likely to be more upset by persistent advances by their superiors—who have the organizational power to coerce them—than by advances from their peers or subordinates, who likely lack that power (Sheets & Braver, 1999). Of course, even if women's reactions to advances did not vary with the status of the initiator, that would not refute the general contention that men's advances were animated by mating motivations.

The above predictions were tested by Colarelli and Haaland (2002), whose study varied the man's power and status. They found that power and status interacted, with harassment ratings increasing as power increased and status decreased. Thus, advances by a low-status man holding power over the woman were most distressing of all. Similarly, Angelone et al. (2009) found that laboratory subjects in an online speed-dating experiment were more willing to receive messages that could be considered sexually harassing from bogus candidates who were physically attractive and had high status than from less-appealing candidates.

The role of sociosexuality in harassment provides further evidence of mating motivations. It is hardly surprising that individuals who measure high on the Sociosexual Orientation Inventory ("SOI") are more likely than low-SOI individuals to engage in sexual harassment, as they are, by definition, oriented toward short-term mating (Kennair & Bendixen, 2012; Sakaguchi & Hasegawa, 2007). However, high-SOI individuals are also more likely to be *victimized.* Observers can detect signs of sociosexuality in others, and high-SOI individuals seem to attract more sexual attention because of their perceived receptivity (Sakaguchi & Hasegawa, 2007). These overtures may be probes to confirm perceptions of their unrestricted sociosexuality and to determine whether short-term sexual relations may be possible (Kennair & Bendixen, 2012). Sexually laden humor may play much the same role in smoking out those with similar mating interests, as sociosexually unrestricted women report greater attraction toward dirty humorists than restricted women do (Medlin et al., 2018). Individuals high in SOI also perceive sexual advances as being less harmful (Klümper & Schwarz, 2020). Yet, some portion of these advances will inevitably be perceived as unwelcome by even high-SOI individuals, and because such individuals will receive more advances, they are likely to experience a greater

number of unwelcome advances even if the proportion of advances that are welcomed by them is also higher. If the purpose of sexual advances were to dominate or oppress, one might expect that low-SOI individuals would predominate among targets, as they would predictably be more upset by the advances (Kennair & Bendixen, 2012). The fact that high-SOI individuals predominate among targets suggests that sex is, in fact, the goal.

Because of the centrality of sexual behavior to reproductive fitness, an evolutionary perspective counsels skepticism about a claim that sexual activities are not "about sex." This skepticism is especially warranted when the claim is that power and sex are unrelated, as dominance and sexuality share similar roots (Herbert, 2015). Throughout human history men have used power to obtain sex, whether coercively or through making themselves attractive as mates. Men with the most power in history routinely surrounded themselves with nubile women whose favors they could command at their pleasure (Betzig, 1986). Male "despots" in the workplace sometimes adopt a similar strategy (though on a much smaller scale and with far less extravagant success), as reflected in the many litigated quid pro quo cases (Browne, 1997, pp. 48–49 n. 227). There is little reason to think that the motivations of a petty workplace tyrant are any less sexual than those of an Eastern emperor.

Power but Not Sex?

Given the existence of behaviors that appear intended to—and sometimes do—result in sexual activity and that are also predicted by sociosexuality, what is the argument that harassment is not really sexual? An early commonly cited study is that of Tangri et al. (1982). They proposed and tested three models of sexual harassment: the "natural/biological" model, which views harassment as a product of natural physical attraction; the "organizational" model, which views harassment as a product of organizational hierarchy whereby individuals use their power to oppress subordinates; and the "sociocultural" model, which views sexual harassment as a product of sex role socialization and the differential distribution of power in society. They concluded that there was evidence to support the latter two models but little to support the first. Following the Tangri study, the idea that there is any significant biological contribution to harassment is often mentioned just to be dismissed (e.g., Juliano, 2007; McDonald, 2012; Pina et al., 2009; Welsh, 1999).

Rejection of the natural/biological model resulted from failure of the data to satisfy the researchers' predictions. They had predicted that harassers and victims would be of both sexes; victims and harassers would be similar in age,

race, and occupational status; both harasser and victim would be unmarried; and the harasser would direct his attention only toward the victim. They also predicted that the behaviors would resemble courtship behaviors, that they would stop once the victim indicated a lack of interest, and that victims would be flattered by the behaviors (although one might wonder why a woman would be flattered by behavior that she considered unwelcome harassment). Because their data did not satisfy those expectations, they rejected the model.

The problem with the Tangri study is that it was not a test of whether harassers were motivated by sexual attraction but rather whether they were seeking long-term mates. But no one has suggested that sexual harassment is mostly "about marriage." What they should have tested was whether the targets possess traits relevant to either long-term *or* short-term mating, since men seeking short-term mates have broader search parameters than those seeking long-term mates (Buss & Schmitt, 1993). A scenario involving a married man's persistent pursuit of sexual favors from multiple younger women of lower status than himself is fully consistent with short-term mating motivations.

Tangri and associates concluded that the disproportionate representation of more-vulnerable individuals among victims was some of the "strongest evidence available in these data against the natural model" (p. 52), an odd conclusion given that vulnerability is a predictor of being targeted for sexual overtures (Goetz et al., 2012). Their apparent view was that it is the vulnerability of young, unattached women rather than their sexual attractiveness that leads to their victimization. Yet it is not clear why a young, naïve single woman is more vulnerable to job threats than a more-savvy fifty-five-year-old woman who has worked for the same employer for thirty years and who has no pension. In any event, the vulnerability of victims does not count against sexual motivations. If the harasser's strategy is to convert his workplace power into satisfaction of his sexual urges, he must focus on targets susceptible to the exercise of that power.

Some researchers imply, without explicitly declaring, that victims are chosen at random, with their sex alone being a sufficient reason for their being targeted. Thus, Workman and Johnson (1991, p. 766) asserted that "some individuals believe only attractive women are sexually harassed" but that "empirical studies do not support this belief, since women in all ranges of attractiveness have reported harassment." Similarly, Gutek (1985, p. 54) contended that sexual harassment "is likely to happen to almost any female worker." These statements imply that victims are chosen without regard to sexual attractiveness, but at most they demonstrate that not all targets are sexually attractive (though they may have been the most attractive targets available). It is noteworthy that after saying that sexual harassment might be aimed at any woman, Gutek goes on to

acknowledge that victims tend to be young and either single or divorced, suggesting that target age and sexual availability are relevant factors after all.

Women sometimes engage in harassment against men, a fact that some argue refutes the natural/biological account (McDonald, 2012; Pina et al., 2009). However, the sex difference in sexual strategies is an average difference. Short-term mating strategies are a larger part of men's sexual repertoire than of women's, but women pursue them also (Buss & Schmitt, 1993). When they do, they presumably are also animated by mating motivations. These critics similarly argue that the existence of same-sex harassment refutes a biological account, although their reasoning is usually unstated. If the existence of male–male quid pro quo harassment disproves the contention that harassers are acting pursuant to sexual urges, one must wonder what the critics think motivates homosexual men to engage in voluntary intimate activities with their lovers.

Berdahl (2007) has argued that it is not young women who "meet gender ideals" who are targeted; instead, it is primarily "uppity" women who exhibit more stereotypically male behavior. These results are said to refute the "mating" model and demonstrate that harassment is designed to punish gender-role deviants. It is difficult to tease out the contributors to Berdahl's results, however, as both sexist comments and sexual coercion (among other things) were counted as sexual harassment. One might imagine that "uppity" women would predominate as recipients of sexist comments suggesting that they do not belong in their jobs, but they might not be overrepresented among targets of sexual coercion. Yet surely Berdahl is correct that women are sometimes targeted by men because they are perceived as encroaching on "male spaces," just as men are sometimes targeted by other men for deviating from masculine ideals (Holland et al., 2016).

A related variant of the sociocultural theory holds that sexual harassment is an attempt by men to exert power out of fear that women constitute a threat to their economic or social standing (Gutek, 1992; Tinkler & Zhao, 2020). This argument implies that the less power men have in society, the more sexual coercion there should be. Yet the most pervasive coercive sex in the history of the master–servant relationship is not between men and women in the modern workplace—where women participate as equals like never before—but rather between a slave owner and his slaves. Female slaves were no threat to their owner's economic or social standing; instead, they were a reflection of it. Nonetheless, sexual relations between slave and owner were extremely common and constituted a major objection of abolitionists to the institution of slavery (Lasser, 2008). The historical record is clear that slave owners did not seek slave women at random for sexual relations. Rather, they preferred those who

possessed the attributes that men typically value in sexual partners: reproductive value as demonstrated by youth and beauty. Consider Stevenson's (2013) description of the slave concubine: "Many were mixed race—African, Native American, European—but the vast majority also were young, beautiful, culturally adept, skilled, sometimes literate and most importantly, physically accessible" (p. 106). The preference for sexual attractiveness was reflected in price, as a prime field hand would sell in New Orleans for $1,800, a top-quality blacksmith would go for $2,500, while a "particularly beautiful girl or young woman might bring $5,000" (Genovese, 1976, p. 416).

An implicit male conspiracy to oppress women has also been posited as the cause of sexual harassment (Farley, 1978). Some researchers have suggested that married women are less likely to be harassed not because men lack interest in sexually unavailable targets but because harassers are honoring the "property rights" of other men (Gutek, 1985, p. 57; Lafontaine & Tredeau, 1986). If correct, men must be parties to an implicit pact under which they will sexually coerce each other's daughters, sisters, and mothers, but they draw the line at their wives. According to this view, male harassers (the majority of whom are married) are willing to honor the marital vows of other men more than they honor their own. This "property rights" argument rests uneasily with Schneider's (1982) finding that "closeted" lesbians—who might have a male partner for all the harasser knows—are subjected to *more* sexual advances than "open" lesbians —whose partners are known to be women—again suggesting that perceived receptivity influences men's overtures (also Wright, 2011). The notion that men are cooperating to compete as a group against women neglects the fact that most of men's competition is against other men—their competitors for sex and status (Buss, 1996).

Much of the foregoing focuses on approach-based harassment, which quite often has sex as a goal. Rejection-based harassment is more likely to be based on hostility or dominance than sexual attraction (Diehl et al., 2012, 2018), though it may or may not flow from sex-based animus. Some men direct harassment toward "uppity women" animated by sex-based resentment of their achievements. However, women engage in the same kind of conduct toward other women. Benenson and Schinazi have noted that across a variety of professions, "women are the first to attack a woman who gets promoted" (Benenson & Schinazi, 2004, p. 329), and successful women are sometimes the greatest barrier to the advancement of women, a phenomenon sometimes labeled the "Queen Bee Syndrome" (Faniko et al., 2021). Resentment of competitors is not automatically sex discrimination simply because of the sex of the persons involved. Even the existence of sexually tinged language is not a clear indication

that hostility is based on sex. Insulting language is often not "sex-neutral," and few epithets are characteristically applied indiscriminately to both sexes (Preston & Stanley, 1987). So, when female employees direct "insults such as slut, ugly, and a bad mother" (Douglass et al., 2020, p. 41) toward their female coworkers, their hostility is not necessarily sex based, just as it does not necessarily reflect sex-based animus when someone refers to a woman as a "bitch" (or to a man as a "prick").

An approach focusing solely on power without resort to psychological sex differences cannot explain why women seldom coerce sex from their subordinates. Some argue that women generally lack the necessary power (Fitzgerald & Weitzman, 1990), but many women hold management and supervisory positions in organizations and faculty positions in colleges and universities. Nonetheless, reported instances of sexual coercion of males by female managers and professors are relatively rare. Less than 1 percent of federal cases over a ten-year period involved sexually based behavior aimed at a male employee by a female supervisor (Juliano & Schwab, 2001), and although men file about 17 percent of EEOC charges (EEOC, 2020), most of them involve a male harasser. One might argue that many men's readiness to engage in casual sex obviates the need for women to coerce them, but that response itself rests on the different sexual psychologies of men and women.

Power and Sexual Priming

Even if men do not use sex as an instrument to obtain power, sex and power are not unrelated, though the relationship is sometimes a nuanced one. Power provides leverage to an individual inclined to extort sex from a victim, such that power leads to sex quite directly. However, power can also operate more subtly. Bargh and Raymond (1995) suggested that men in supervisory positions who pursue sexual favors from subordinates often do not realize they are exploiting their power. Rather, their sexual pursuit may arise because of an unconscious link between power and sex. When a man having an "automatic power-sex association" is placed in a position of power over a woman, the association enhances his perceptions of both her sexual interest and sexual attractiveness (Bargh et al., 1995; Zurbriggen, 2000). The superior may feel attraction toward the subordinate and then, when she acts in a deferential and friendly manner, infer that the attraction is reciprocal. This heightened attraction does not appear to result simply from a desire to dominate. Kunstman and Maner (2011) found, for example, that the expectation of sexual interest from a subordinate was especially heightened if the subordinate was romantically available and had an

unrestricted sociosexual orientation, supporting the existence of a mating motivation.

The power-sex association suggests that sexual-harassment training might be modified. Much current training focuses on warning men not to exploit their power over subordinates to coerce sex or simply instructing that sexual relationships between supervisors and subordinates are inappropriate. These messages may not be terribly effective in modifying the behavior of a man having the power–sex association. If the man is unaware that it is his power that creates both his attraction and his perceptions of his target's receptivity, he would likely not consider his conduct to be exploitive. If he perceives, whether correctly or not, that the relationship is one of mutual attraction, he may view institutional strictures against supervisor–subordinate relationships as casting him in the role of Romeo in a scenario of forbidden love. Educating men explicitly that their power may result in misperceptions might be more effective.

Although power is unquestionably an important component of some forms of sexual harassment, especially quid pro quo harassment, mating motivations are hard to deny. Such motivations also underlie much hostile environment harassment, particularly that involving unwanted sexual advances and requests for dates. The claim that "the goal of sexual harassment is not sexual pleasure but gaining power over another" (Bravo & Cassedy, 1992, p. 16) may thus get the relationship exactly backward. The focus on power to the exclusion of sex appears to be a side effect of the fact that most of the scholarship on harassment has been from the woman's (victim's) point of view. From the victim's perspective, it may seem like all power and no sex, but if the goal of sexual harassment regulation is to shape the harasser's actions—rather than simply to provide a remedy to the victim after the fact—an accurate perception of *his* motivations is essential. To say that sexual harassment is only about power and not about sex is like saying that bank robbery is only about guns and not about money.

The "Reasonable Person" or the "Reasonable Woman"?

The choice of standard for determining whether a hostile environment exists could also benefit from an evolutionary perspective. The law requires the plaintiff to prove both that *she* experienced the environment as hostile (a subjective inquiry) and that the environment was "objectively" hostile (*Harris v. Forklift Systems, Inc.*, 1993). In applying the objective prong, the question arises whether a sex-specific inquiry should be employed. That is, should the environment be judged from the perspective of a reasonable person, or, when the

plaintiff is a woman, should it be judged from the perspective of the reasonable woman (Wiener & Vardsveen, 2018)?

Proponents of both positions can muster logical arguments. Those favoring a reasonable-person standard argue that a reasonable-woman standard is paternalistic and holds men to a standard of conduct that they may not understand (Adler & Peirce, 1993). According to one court, a reasonable-woman standard "may reinforce the notion that women are 'different' from men and therefore need special treatment—a notion that has disenfranchised women in the workplace" (*Radtke v. Everett*, 1993, p. 167 n.37). Arguments in favor of a reasonable-woman standard, on the other hand, have relied upon just the differences that the *Radtke* court was reluctant to reinforce. As one court stated, "conduct that many men consider unobjectionable may offend many women" (*Ellison v. Brady*, 1991, pp. 878–879). Despite variability in women's viewpoints, the court said, women "share common concerns which men do not necessarily share" and "women who are victims of mild forms of sexual harassment may understandably worry whether a harasser's conduct is merely a prelude to violent sexual assault." In selecting between these two standards, it is instructive to consider just how different men's and women's perspectives actually are.

Sex Differences in Sexual Perceptions

Men and women have substantially divergent views about sexual matters in general and sexual harassment in particular. Although there is agreement about the most serious forms of harassment, such as coerced sex (Rotundo et al., 2001), the sexes often differ over milder sex-related conduct—such as touching, sexual comments, or sexual advances (Rothgerber et al., 2021). One widely reported finding is that a substantial majority of women would be offended by sexual overtures at work, whereas a substantial majority of men would be flattered (Gutek, 1985; also Berdahl, 2007). Similarly, Berdahl and Aquino (2009) found that 46 percent of men and 10 percent of women found sexual behavior at work to be fun and flattering. A study of attitudes about workplace emails similarly found that men rated emails containing sexual propositions to be "somewhat enjoyable," but women found them to be very offensive (Khoo & Senn, 2004, p. 210; also Matthews et al., 2018). Thus, it seems, where a man might see "opportunity," a woman sees "danger," as illustrated by Struckman-Johnson and Struckman-Johnson's (1994, p. 401) striking finding that a substantial number of men "viewed an advance by a good-looking woman who threatened harm or held a knife as a positive sexual opportunity."

Key to sex differences in perspectives on sexual matters is the principle of "relative parental investment" (Trivers, 1972) and the "sexual strategies theory" that flows from it (Buss & Schmitt, 1993). In short, because of asymmetries in obligate parental investment, men devote a greater share of their reproductive effort to short-term mating. Because men see the world "through sexual glasses," they tend to see situations as more sexually oriented than women do. In their interactions with women, men often perceive sexual interest where women perceive only friendliness (Abbey, 1987, 1982). The tendency of men to interpret friendly behavior as an indicator of sexual interest coupled with women's tendency to interpret sexually interested behavior as mere friendliness leaves much room for misunderstanding.

The converse of men's bias toward perceiving sexual interest on the part of women is women's bias toward perceiving sexual threat on the part of men where the risk of coercion exists (McKibbin & Shackelford, 2011; Thornhill & Palmer, 2000). Losing control over the choice of sexual partners, even momentarily, creates a far greater risk for women than for men. Thus, behavior that may appear friendly in an unthreatening atmosphere may be viewed as threatening if autonomy is constrained.

Differences in perception that lead to misunderstanding between the sexes are explained by "error management theory" (Haselton & Buss, 2000). In making judgments under uncertainty, the human mind is not interested solely in reducing errors but also in minimizing the costs of error. Because errors are not all equally costly, selection can create psychological adaptations that are biased to result in more numerous but less costly errors. A man who makes advances only when he is certain that his interest is reciprocated would predictably have less success than a man who proceeds if there is some chance that the woman will be receptive. In ancestral environments, most women would have been married, pregnant, or lactating, so that men's opportunities to mate with fertile females would have been relatively rare, making missed opportunities particularly costly. Men are thus predisposed to false positives (inferring interest that does not exist) rather than false negatives (failing to recognize genuine interest). In contrast, because of the fitness costs to a woman who loses control over her mating choices, natural selection would favor a woman's cautiousness about sexual coercion. It is better to infer a threat of sexual coercion that does not exist than to ignore one that does, leading to a bias toward false positives about threat. Thus, both sexes seem to be adaptively biased in favor of making the less costly choice, and those biases have real-world consequences.

Individual Differences

Recognition of average sex differences in perceptions should not obscure either commonalities between the sexes or individual differences within the sexes. Both sexes generally agree on the harassing nature of more severe conduct, although they often disagree about milder and more ambiguous conduct (Rotundo et al., 2001). Members of both sexes often enjoy "social sexual behavior" at work, such as flirtation, gentle touching, sexual innuendo, and off-color jokes (Aquino et al., 2014), although women are generally less likely than men to enjoy a sexualized workplace (Berdahl & Aquino, 2009; Khoo & Senn, 2004). Indeed, some women actually feel empowered by sexualization (Erchull & Liss, 2013a, 2013b; Liss et al., 2011). Thus, a given environment might be perceived as unpleasant by some "reasonable women" and pleasant by others.

Individual-level traits play an influential role. Men high in sociosexuality seem to be most prone to engage in unwelcome advances (and high-SOI women are disproportionately their targets) (Kennair & Bendixen, 2012), apparently because high-SOI men are particularly likely to exhibit a bias toward overperception of sexual interest (Perilloux et al., 2012). Those possessing the dark triad personality traits (narcissism, Machiavellianism, and psychopathy) unsurprisingly tend to be high in sexual harassment proclivity (Zeigler-Hill, et al., 2016). Somewhat more surprising is the fact that men *low* in dark triad traits seem to be the most affected by power priming, apparently because those high in such traits are chronically inclined to exploit power and need no priming to do it (Stockdale et al., 2019). Power priming exerts special influence on chronically low-power individuals who are newly placed in a position of power compared to individuals with chronic high power (Williams et al., 2017). Given the role played by personality, it is not surprising to find that many sexual harassers are serial offenders (Cantalupo & Kidder, 2018; Lucero et al., 2006).

Misperceptions on the Job

When women and men go to work, they take their sexual psychologies with them, creating ample opportunities for miscommunication. The inherent ambiguity of courtship communication is exacerbated in the workplace by the need for continued association (Stockdale, 1993). If the target's message is ambiguous, the perpetrator may interpret her behavior as welcoming (Yagil et al., 2006). Women often give pretextual reasons for rejecting dates, such as identifying something about the specific date rather than their general lack of interest in the suitor (Baumeister & Dhavale, 2001). If a woman makes excuses when she declines an invitation from a male coworker (she is busy, feels sick, etc.), she may think that she has conveyed her lack of interest and that will be the

end of it; he should just “take the hint” and stop. These “soft rejections” may be designed to spare the man’s feelings or to avoid conflict with, and potential retaliation from, a coworker or superior. He, on the other hand, may just think his timing was bad and rationally conclude that better days are ahead—the next time she may not be busy or will be feeling better. This lack of clarity may result in the “persistent requests for a date after repeated refusals” that end up being the basis of sexual harassment charges. He may find himself asking, “Why didn’t she just tell me she didn’t want to go out with me?” while her response might be, “I thought I did.”

The risk of miscommunication is exacerbated by the common perception that women often “play hard to get,” meaning “yes” even if they say “no” (Muehlenhard & Hollabaugh, 1988). As Mealey (1992) noted, the fact that “females are selected to be coy will mean that sometimes ‘no’ really does mean ‘try a little harder.’ ” Because many men know that “no” can be a prelude to “yes,” they may persist even when “no” was actually intended to mean “no.” The inherent ambiguity of such situations means that it is naïve to assert that “sexual harassment allegations are either true or false” (O’Donohue & Bowers, 2006, p. 56) in the way that one might make such a claim in a lawsuit that turns on whether a traffic light was red or green.

Safeway Corporation learned about sex differences in perceptions the hard way after it implemented a plan to foster customer loyalty in 1998. Under this program, clerks were directed to smile at customers, make eye contact with them, and call them by name (Ream, 2000). Some female clerks filed sexual harassment charges claiming that the required behavior prompted male customers to interpret their behavior as flirtatious, leading to sexual comments, propositions, and even stalking. Exacerbating the problem, the Safeway policy forbade employees to discontinue the friendly behavior when customers responded inappropriately, thus resulting in further encouragement of the unwelcome attention. The harassment charges were dropped when Safeway agreed to modify the policy.

Much of the academic literature on sexual harassment proceeds under the assumption that sex has no place at work. Litigated sexual harassment cases, playing out in the marbled halls of the judicial system, accentuate this tendency, as the solemnity of the venue makes discussions about sexual matters seem almost as out of place as they would be in a church. But the real workplace is a different place from this stylized, sexless paradigm. An off-color joke that provokes a gasp in a courtroom may be daily fare that is enjoyed in many workplaces. An increasing literature documents the positive aspects of sexually tinged behavior at work. Flirtation at work can provide a source of enjoyment

and can operate as a buffer against work-related stress for all parties involved (Sheppard et al., 2020). Some of the behavior is what Watkins et al. (2013) have called "strategic sexual performances"—sexual behavior that acts as an ingratiatory tactic, such that "men and women trade sexual performances at work to get what they want, with it being neither unwanted nor necessarily dysfunctional" (p. 177). Such behavior can even enhance organizational performance, although it may disadvantage women who either cannot or do not wish to engage in such behavior, as well as men, who are not in a position to compete in that way. Although often harmless, when a woman draws on what Hakim (2010) refers to as her "erotic capital," there is always the possibility that the man may interpret her flirtatious behavior as being more than just a social lubricant but also an indication of sexual interest.

When sex differences in perspective lead to miscommunication—that is, when the man reasonably (from the perspective of the reasonable man) makes sexual overtures that a woman reasonably (from the perspective of the reasonable woman) finds disturbing or even threatening—who, if anyone, is to blame? The usual answer is that the man is responsible; after all, he has made a sexual advance that was "unwelcome," and sexual harassment doctrine, at least in the United States, does not make the man's intent especially relevant (Browne, 1997). However, when a person reasonably receives a message different from the one that the sender reasonably intended to convey, both subjects are engaging in miscommunication.

An evolutionary perspective demonstrates that the notion of a "reasonable person" unmoored by sex is incoherent. When it comes to sex, there are reasonable women and reasonable men (and, of course, their opposites). These insights might productively be recruited in designing sexual harassment training. Most sexual harassment training provides a broad definition of harassment and focuses on educating men not to engage in it. But if some sexual harassment results from miscommunication, education might be directed to both potential harassers and potential victims. Not only might potential harassers be counseled that their behavior, even if well meaning, can be misunderstood, potential victims might likewise be counseled that they may be sending signals that they do not intend and also that conduct to which they are reacting negatively might not be intended the way they perceive. Avoiding miscommunication might be a better goal than simply heightening sensitivities. Although sexual harassment training is often evaluated by the extent to which it causes its participants to identify conduct as harassment (Antecole & Cobb-Clark, 2003; Blakely et al., 1998; Roehling & Huang, 2018), heightening sensitivity might be a counterproductive goal (Dobbin & Kalev, 2019).

Does the Choice of Standard Matter?

Although a reasonable-woman standard seems most consistent with human psychology, the choice of standard may turn out to have little effect in the real world. Some laboratory studies have found a modest effect, with subjects using a reasonable-woman standard being somewhat more likely to label conduct as harassment (Blumenthal, 1998; Gutek et al., 1999; Wiener & Hurt, 2000). Whether the findings of these laboratory studies are relevant to real-world cases is unclear (see Cesario, 2021). In actual trials, the jury will have ample opportunity to get to know the plaintiff, so sex may be substantially more salient to them than to laboratory subjects reading hypothetical scenarios about unknown people, which may trigger a lesser visceral response. A study of all reported federal cases in the United States over a ten-year period found no difference in outcomes between cases using the two standards (Juliano & Schwab, 2001) in those cases where it could be determined what standard was used. A different study found, in contrast, that cases in reasonable-woman jurisdictions were slightly more likely to favor the plaintiff (Perry et al., 2004). Whether that small effect is attributable to the jury instructions is unclear, however. It could simply be that "liberal" jurisdictions are more likely to use a reasonable-woman standard *and* more likely to find plaintiffs in harassment cases. It also may be that jurors are simply not particularly influenced by their instructions in these cases. A recent study found that subjects' assessment of whether particular conduct constituted sexual harassment was unaffected by which of two different definitions of sexual harassment they were given or even whether they were given any definition at all (Rothgerber et al., 2021).

The standard's apparent lack of impact is probably not because judges and jurors interpret the terms "reasonable person" and "reasonable woman" identically. More likely, they are implicitly using a reasonable-woman standard irrespective of how the standard is articulated. In the typical case, juries are presented with evidence (including the plaintiff's testimony) and asked to decide whether, considering the totality of the circumstances, it objectively constituted an abusive environment for her. Whether specifically instructed to or not, it is likely that one of the circumstances that will influence them are the sexes of the alleged harasser and the plaintiff. Thus, the folk psychology of jurors may resolve a problem that turns out to exist only in the minds of academics.

The formal standard may matter less than the identity of the persons applying it. Whatever the articulated standard, it is judges and juries who must apply it in the context of an actual lawsuit, and males and females may apply a given standard differently. Most sexual harassment cases that go to trial are decided by

a jury. The fact that women in general identify a broader range of conduct as harassment implies that female jurors may be more likely than male jurors to identify a particular course of conduct as harassment. However, there are no good data on the sex composition of juries and outcomes in actual cases, and such data would be very difficult to obtain since juror information is not widely available. Although the conventional wisdom is that female jurors will be more favorable toward female plaintiffs, it is legally impermissible for a lawyer to attempt to obtain a jury sympathetic to his client's cause by relying on sex in selecting jurors (Toro, 2015).

There is equivocal evidence for a sex effect among judges at both the trial and appellate levels (Harris & Sen, 2019). The trial judge's principal functions are to decide pretrial motions relating to discovery and admissibility of evidence and motions that determine whether the case should proceed to trial. There is evidence that female judges are somewhat more plaintiff-favoring than male judges in ruling on these motions in harassment cases (Knepper, 2018). Likewise, there is some evidence that female appellate judges are also more favorable to sexual harassment plaintiffs. In an analysis of sexual harassment cases in federal appellate courts over a three-year period, Peresie (2005) found that female judges on three-judge panels were almost twice as likely to vote in the plaintiff's favor than male judges (although the female judges were still more likely to vote in favor of the defendant than in favor of the plaintiff). Using a different large-scale database, however, Boyd et al. (2010) found no sex effect in sexual harassment cases (though they did find one in sex discrimination cases). Confounding the results in these studies is that many court rulings in harassment cases involve issues other than whether an environment is hostile. So, the most one can say is that it would not be surprising to find that male and female judges differ somewhat in their assessments, but the jury is still out.

Conclusion

Sexual harassment is a multifaceted phenomenon arising from a variety of motivations. Some is based on hostility to women in the workplace and some may be based on hostility to a particular woman (which in turn may or may not be based upon her sex). Much of it, however, is a product of mating psychology. It does not minimize the harm caused by sexual harassment to recognize that fact.

The contention that sexual harassment is only about power and not sex is difficult to square with the evidence. When a supervisor extorts sex from a subordinate or when one coworker directs persistent advances toward another,

there is little reason to believe that the motivations are not sexual. Targets of such behavior tend to be young, attractive, unattached women, who are also typically the recipients of sexual advances outside the workplace. Women high in sociosexuality are at greater risk of such behaviors, apparently because they give off signals of receptivity, and men high in sociosexuality seem to be disproportionately represented among harassers. Mating motivations in these cases seem fairly clear.

Yet power surely can play a role. Quid pro quo harassment can only be employed by someone with greater power than the target. Moreover, power may be implicated even where coercion is not intended. An unconscious power–sex association leads some men to experience heightened attraction to subordinates and heightened perceptions of reciprocal attraction. These men may then make what they believe to be welcome advances toward targets who do not find them so. The claim that in these cases the goal "is not sexual pleasure but gaining power over another" (Bravo & Cassedy, 1992, p. 16) is simply hard to credit, though it may well be true in rejection-based harassment cases.

An understanding of the different sexual psychologies of men and women—especially differences in short-term mating orientation—also sheds light on the choice between the reasonable-person or reasonable-woman standards. Men tend to see the world through more sexualized lenses than women do, causing the sexes to perceive sexual matters somewhat differently. Error-management theory explains why a man may overestimate a woman's interest in him and also why a woman may overestimate the threat a man poses to her and react negatively to overtures that are intended as benign. Consequently, an androgynous standard makes little sense. In sexual matters, there are "reasonable men" and "reasonable women," reflecting average sex differences in sexual psychology; there is not a sexless "reasonable person."

Given that current sexual harassment training is often ineffective or even counterproductive (Tinkler et al., 2007), training might be modified to educate men and women about sex differences in perspectives to avoid miscommunication rather than simply heightening sensitivity to what may be ambiguous or misunderstood conduct. Expert witnesses in sexual harassment cases, who virtually all come from the "social construction of gender" school (see O'Connor, 2006), might provide greater assistance to the jury if they incorporated a more robust theoretical perspective.

A realistic view of human nature suggests that as long as men and women inhabit the same workplaces, they will interact as human beings who do not leave their sexual psychologies at the door (Watkins et al., 2013). Large numbers of people find romantic partners at work (Boyd, 2010; Hoffman et al., 1997), and

policies aimed at requiring employees to act as sexless drones are unlikely to be effective. Even if effective, such policies may be no boon to employees. Women probably have the most to lose from a "Puritanization" of the workplace, as men's fear of being on the wrong end of a sexual harassment complaint may result in exclusion of women from mentoring and bonding opportunities (Elsesser & Peplau, 2006; Hewlett et al., 2010; Kreis, 2020).

Some believe that recognition of the evolutionary underpinnings of these behaviors necessarily means that they are inevitable or morally correct (McDonald, 2012) or that such recognition "trivializes" sexual harassment (Pina et al., 2009, p. 133). But this reasoning embodies the naturalistic fallacy (Curry, 2006); behaviors with origins in our evolved psychologies can be recognized as social pathologies even if they do not reflect psychological pathologies (Buss, 2005; Thornhill & Palmer, 2000). Their evolutionary origins do not render them immune to modification. If our evolved psychology is the source of sexual harassment, we can take solace in the fact that it is also the source of our desire to combat it. This more nuanced understanding provides us the means to more effectively manage it.

Note

1. Although both men and women can engage in (and be victimized by) sexual harassment (Douglass et al., 2020), most of the literature, as well as existing case law, has focused on male perpetrator/female victim cases; unless the context indicates otherwise, the discussion will focus on such cases.

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CHAPTER
27

Sexual Coercion

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Abstract

This chapter reviews evolutionary theory and research on sexually coercive behavior. Such actions are diverse with respect to severity, types of acts, targets, and individual difference characteristics, and thus a comprehensive theoretical framework is needed to account for such diversity. Sexual selection has been prolific in explaining variation in sexual coercion between and within species, though controversies and criticisms stifled its application to humans. Ultimately, sexual coercion is motivated by a mating psychology that causes, or is a consequence of, sexual conflict, and can be understood in terms of psychological adaptations, by-products, and disorders. Among humans, understanding proximate and ultimate causes of sexual coercion has implications on assessing and treating sexual offenders.

Key Words: sexual coercion, sexual conflict, sexual selection, rape, adaptation, byproduct, disorder, typology

Evolution of Sexual Coercion

Darwin's seminal theory of evolution by natural selection to explain biodiversity has driven and integrated research in the biological sciences, including psychology. By understanding psychology from principles and theoretical models established in the natural sciences, psychologists have made significant advances in our understanding of mind and behavior. In particular, Darwin's extension of natural selection to sexual selection showed how a simple process could explain the vast number of sex differences observed across all sexually reproducing species. This chapter reviews how Darwinian principles

have been used to understand one such sex difference—sexual coercion.

Evolution by Natural and Sexual Selection

Traits that confer a reproductive benefit become more prevalent over successive generations. Often, this selection pressure results in traits that are complex, precise, efficient, reliable, and economical (Williams, 1966). These adaptations, sometimes called mechanisms, are functional because they help organisms overcome specific barriers to survival and reproduction. Sexual selection, first described by Darwin in 1859 and later elaborated in 1871, is a variant of natural selection where it suggests that when barriers to survival and reproduction differ between the sexes, we might expect the sexes to evolve different adaptations. As Darwin described, males with traits that assist with outcompeting rivals "for the possession of the other sex" become more prevalent over successive generations. These include physical traits and behaviors that help with attacks and defenses (e.g., antlers on a stag or fighting between male salmon). Darwin also identified how sexual selection could function through mate choice—where male-specific traits could evolve because females prefer them (e.g., size and color of plumage and birdsongs).

These principles have driven scientific research in all areas of biological life, including important puzzles about cooperation and conflict. Sexual coercion, a prevalent form of conflict, emerged as an important topic of evolutionary inquiry because of its pervasiveness across taxa, variation within species, and clear sex differences. The goal of researching sexual coercion was to identify why such harmful behavior to victims exists, and how mechanisms associated with this behavior might function.

Sexual Coercion

Among nonhumans, sexual coercion refers to aggressive actions by males that increase the probability of future mating over other males. In its various forms, sexual coercion is observed across many vertebrates and invertebrates (Watson-Capps, 2009). Historically, two lines of research addressed sexual coercion from an evolutionary framework: (1) sexual coercion was treated as a third mechanism of sexual selection and (2) sexual conflict theory described sexual coercion as both a cause and consequence of sexual conflict (see section "Sexual Conflict and Sexual Coercion"). Watson-Capps (2009) synthesized the two by suggesting that sexual conflict regarding when and with whom to mate

created the conditions for sexual coercion to evolve, and sexual coercion also maintains sexual conflict. A third evolutionary approach to sexual coercion, focusing mostly on human rape, came from evolutionary psychology.

Among humans, sexual coercion is typically defined as the nonconsensual use of force, threat of force, or harmful manipulation to obtain sex (some manipulation, such as sexual coaxing, may not be harmful; see Camilleri et al., 2009). As with nonhumans, sexual coercion among humans is pervasive—it is observed across all known cultural groups and has been documented throughout written history (Brown, 1991; Lalumière et al., 2005). Much of the evolutionary literature has focused on stranger, marital, and acquaintance rape, though other types of sexual coercion have received at least some attention.

Sexual Conflict and Sexual Coercion

Sexual conflict is a middle-level evolutionary theory that addresses how traits could evolve when it benefits one sex while costly to the other sex. This conflict occurs in one of two ways: *intralocus sexual conflict* is when both sexes share the same trait but the trait has conflicting fitness outcomes (i.e., allele variation occurs at the same locus), whereas *interlocus sexual conflict* is when different traits in each sex are in conflict (i.e., alleles from different loci are in conflict). Sexual coercion may be a type of interlocus sexual conflict because a trait in one sex (male sexual coercion) is in conflict with a trait in the other sex (female choosiness).

Sexual conflict has been used to understand both direct and indirect forms of sexual coercion in nonhuman species (Muller & Wrangham, 2009). *Direct sexual coercion* is when actions increase the probability of mating, such as forced copulation, harassment (i.e., male sexual persistence), and intimidation (i.e., intimidate by punishing refusal). *Indirect sexual coercion* is when actions minimize mating options for females, such as herding (i.e., male aggressively separates females from other males), punishment (i.e., punish female's interaction with other males), and sequestration (i.e., male aggressively removes a female from their social group). Both direct and indirect forms of sexual coercion are examples of sexual conflict because they increase the male's probability of mating while incurring costs to females by removing their choice in when and with whom to mate.

Applying these concepts to humans has gained traction in recent years (Buss, 2017; Shackelford & Goetz, 2012). For example, Camilleri and Quinsey (2012) reviewed how direct and indirect sexual coercion could appear in intimate relationships. Direct coercion, which immediately increases the probability of

mating, includes *forced in-pair copulation* in response to cuckoldry risk or *harassment* in response to sexual refusal. Indirect sexual coercion, which decreases the probability of female extra-pair mating, may occur as *herding/sequestration* when males use various mate-retention behaviors, such as vigilance, concealing a mate, threatening rivals, and monopolizing partner's time. *Punishment* may also occur when males aggressively respond to suspected infidelity or see their partner with another male. Much of the empirical literature is consistent with these explanations: mate guarding increases when partners are fecund, men use violence in response to females trying to leave a relationship, sexual coercion is associated with cuckoldry risk, and men who are sexually jealous are more prone to using violence toward their partner. In all cases, the behaviors are consistent with the view that they attempt to limit women's reproductive options through coercive control, which increases their own probability of mating (or reduces a rival's probability of mating). These actions may promote reproductive success because they are largely directed toward younger, and hence fertile, females, particularly those who may be pursuing other relationships. Though the literature is consistent with these hypotheses, very few hypotheses have been directly tested among humans.

A third form of sexual coercion is *infanticide* because in some species, killing a female's offspring ends her lactational amenorrhea, which increases the probability of mating. This form of sexual coercion is not likely true among humans since infanticide is rare, and no known association exists between infanticide and increased opportunity of mating with the victim's mother.

Evolutionary Psychology and Rape

A parallel literature in evolutionary psychology attempted to understand stranger and acquaintance rape by testing hypotheses about proximate and ultimate causes of such behavior. Symons (1979) theorized that rape results from a male sexual psychology that motivates them to pursue impersonal sexual relations, so when faced with sexual refusal, men resort to rape in circumstances where the costs of such behavior are low. Symons cited elevated frequency of rape in war as an example of this. That same year, Alexander and Noonan (1979) suggested that if ovulation is concealed, and sexual receptivity is not related to ovulation, then forced mating with an unreceptive female would be as likely to result in fertilization as mating with a receptive female. Mating refusal may also indicate the female is pair-bonded, and so any offspring resulting from the rape may unknowingly be cared for by a cuckolded male. Consensual mating is the most common strategy because it has fewer risks. Many of the earliest

evolutionary explanations are variants of rape as an adaptive response to *mate deprivation*—men who face lower probability of mating resort to using force. Thornhill (1980) suggested that forced copulation could evolve in species where males control resources that assist with female fitness, which means some men who compete for these resources will lose out and may resort to forcing sexual activity.

Thornhill and Thornhill (1983) continued to develop these ideas by drawing from theoretical models of sexual conflict, identifying parallels between human rape and nonhuman forced copulation, and reviewing empirical research. Sexual conflict was very new at the time, but Thornhill and Thornhill recognized its application to humans by identifying how men's coercive control of women's reproductive options and forced insemination, though increasing men's reproductive success, comes at a significant cost to women. Generally, Thornhill and Thornhill hypothesized that rape evolved as a facultative response where less desirable males, due to lower status and failed competition, resort to coercive sexual acts. This hypothesis is more commonly referred to as the *mate deprivation hypothesis*. Some evidence they cited to support their hypotheses included (1) younger women, who have higher reproductive value, are more likely to be victims[1]; (2) younger men, due to being at an age of higher competition, are more likely to be rapists; (3) men who are more economically disadvantaged are more likely to rape, due to having a lower probability of successful mateships; and (4) rapists are aware of their lower status.

In the same volume, Shields and Shields (1983) published their evolutionary explanation of rape by discussing how it could have evolved relative to other reproductive strategies. They argued that men have one of three mating strategies: *honest courtship* (also called cooperative bonding), where men give honest signals of quality, resources, and intention to provide parental investment; *deceitful or manipulative courtship*, where men give dishonest signals of quality, resources, and intention to provide parental investment; and *rape*, where men use sexual force because even a small chance of fertilization could lead to the selection of such a strategy. Because the payoffs of each strategy are not equal, all men have the capacity to use each of them depending on circumstances that change the costs and benefits. Rape is the least common strategy because of the steep costs, such as women's resistance and risk of injury and retribution. Though not described using the language of sexual conflict, Shields and Shields also noted that rape may have reproductive benefits for men with costs for women. Shields and Shields' theoretical explanations complement Thornhill and Thornhill's because they both suggest rape is a conditional strategy that may occur when benefits outweigh the costs, such as when men are mate deprived.

Other evolutionary-minded researchers suggested that rape could occur as a by-product of other mating adaptations, such as men's preference for impersonal sex, persistence in pursuing sex, greater arousal to visual stimuli, higher sex drive, interest in multiple mating partners, and lower discrimination of mating partners (Palmer, 1991; Symons, 1979). Though the by-product hypothesis has not been given as much attention, the concept of sexual coercion as a by-product of other psychological mechanisms is an important consideration. A potential reason for the lack of attention is the difficulty and confusion in testing for by-products. For example, Camilleri (2012) identified how sometimes the data used to support rape as a by-product have also been used to support rape as an adaptation. Despite the paucity of evidence, by-products potentially explain some forms of sexual coercion (see section "Sexually Coercive By-products").

Criticisms

Historically, feminist and evolutionary explanations of sexual coercion were at odds and the literature sometimes antagonistic. Feminist approaches viewed rape as one of many violent acts men use to promote and maintain a patriarchal society, and that sexual motivations were either not important or secondary to violence (Brownmiller, 1993), which countered evolutionary models that focused on the potential reproductive function of forcible rape. The debate reached a tipping point after the publication of Thornhill and Palmer's *A Natural History of Rape*, where in addition to outlining their evolutionary explanation of rape and reviewing the empirical literature, they provided a scathing criticism of feminist theory and the social sciences. Though the publication of this book was arguably the first to share evolutionary explanations of human sexual violence to a wider, more general audience, there was also widespread criticism, not surprisingly from social scientists and feminists, but also from evolutionary-minded researchers as well. Many of the major criticisms were published in Travis's (2003) edited volume, *Evolution, Gender, and Rape* and across academic journals. Unfortunately, these criticisms lacked a cohesive argument, included opinion pieces that shared incorrect facts, misunderstood how evolution and genetics work, misrepresented evolutionary psychology, and argued using the naturalistic fallacy, among many other problems (Lalumière, 2006; Palmer & Thornhill, 2003a, 2003b; Thornhill & Palmer, 2002). Poor criticisms failed to progress our knowledge on the topic, and the negative publicity may have stifled progress in studying sexual coercion from an evolutionary framework as young academics and funding agencies may have viewed the topic as too controversial (Lalumière, 2006). Criticisms must be guided by good methodology, sound

understanding of theory, and a fair review of empirical research on sexual coercion if we aim to adequately address such harmful behavior.

It should also be noted that traditional approaches to understanding sexual coercion are not inherently in conflict with evolutionary approaches, since traditional approaches investigate proximate causes (i.e., immediate causes) whereas evolutionary approaches also investigate ultimate causes (i.e., ask *why* such causes exist in the first place; see Goetz et al., 2008; e.g., Shields & Shields, 1983; Vandermassen, 2011). Shields and Shields were aware of a common belief at the time that rape is not about sex but about aggression. Shields and Shields addressed this point by highlighting how rape could be selected if it increased reproductive success (ultimate cause), and that aggression is a way to overcome resistance in order to obtain sex (proximate cause). Goetz et al. (2008) similarly bridged the gap between evolutionary and domination/control explanations of partner rape. Recognizing the difference between ultimate and proximate causation is an important way to reconcile the differences between approaches to sexual offending and gives structure on how to move forward. Not all attempts to consolidate social science with evolutionary models on rape have been successful, however. Integrated models were also proposed to appease the divide between evolutionary and nonevolutionary explanations but fell short on truly integrating them.

Integrated Models

Some models tried to reconcile theoretical differences between evolutionary and nonevolutionary accounts of sexual coercion by integrating them. These models included Ellis's (1989, 1991) synthesized theory of rape, Malumuth's (1996) confluence model, and Ward and Beech's (2006) integrated theory of sexual offending. Malamuth's confluence model suggests that early experiences influence delinquency, which then impacts promiscuity and attitudes toward violence, leading to hostile masculinity, which results in sexual coercion. These factors are believed to interact to lead to sexual aggression. Evolution plays a part in this model by accounting for sex differences in impersonal sex, which may lead to arousal toward an unwilling partner, and using dominance/hostility as a way to control women's reproductive options. Similarly, Ellis's model suggested that feminism accounts for power and control, evolution for sex differences in sexual drive, and behaviorism accounts for learning through operant conditioning and imitation. Ward and Beech's model is the most ambitious attempt to integrate various theoretical models and factors associated with sexual offending (what they call "theory knitting"). Their model suggests

that essentially every process or factor plays a role in sexual offending, including evolution, genetics, social/cultural, personality, social learning, cognition, motivation, perception, and memory, among others, but it provides no framework on *why* these factors should be associated to each other or to sexual coercion. A primary issue across all three models is that they treat evolution as a separate process or "biological" factor from other contributing factors, such as environmental or process variables, attitudes, and learning. Here we have a misunderstanding of how evolution works on human psychology as evolution should explain why and how each factor in the model is associated with sexually coercive behavior. Psychology cannot function independent of its biology—thoughts, feelings, and behavior all require biological structures and processes. Biological/psychological traits were selected through evolutionary processes to overcome environmental challenges, and some traits evolved to be responsive to environmental variation, so arguments that evolution somehow parallels psychological, biological, or environmental causes of sexual coercion are not tenable. Since all behaviors require psychological mechanisms, and all mechanisms are a product of evolutionary processes (see Buss, 1995), we cannot separate evolution as an alternative path to behavior from their proximate causes. Integrated models will continue to lack validity if they treat evolution as an independent pathway or explanation, rather than a complementary, overarching one.

Evolutionary-Informed Typology of Sexual Offending

There has been steady growth of evolutionary models and hypotheses about various sexually coercive actions. Generally, this literature has shown that (1) the diversity in types of sexually coercive behaviors require domain-specific explanations, and (2) even one type of sexually coercive act, such as stranger or acquaintance rape, may occur for different reasons. Despite some progress, there is little coordination between these works. To address these points, Camilleri (2012) outlined a typology of sexual offending based on two dimensions: etiology of the trait (i.e., adaptation, by-product of an adaptation, or a disordered adaptation) and how it functions. Function refers to whether the trait is *obligate* (i.e., trait is not responsive to environmental variation—variation in the trait is due to variation in genes); *facultative-fixed* (trait is permanently expressed after exposure to a certain environment), or *facultative-flexible* (the trait is temporarily expressed after exposure to a certain environment) (see also Camilleri & Stiver, 2014, for a revision of the typology). Not only does the typology help organize the literature, moving forward it provides researchers a way to clearly identify

how their hypotheses fit into this larger body of work (see table 27.1). In the next section, I review theoretical explanations of each hypothesized sexual offender type and the weight of empirical literature supporting it.

Sexually Coercive Adaptations

If sexual coercion is an adaptation, there needs to be evidence that it serves a particular function that probabilistically increased fitness during the time in which it evolved. Selection pressures over evolutionary time shape adaptations to be complex, precise, efficient, reliable, and economical (Williams, 1966). Testing for some of these characteristics among humans is rather difficult because experimental manipulation or longitudinal research is both unethical and unfeasible. Still, evolutionary psychologists can draw from a wide variety of sources, such as genetics, phylogenetics, physiology, psychology, medicine, anthropology, and of course theory to systematically test for adaptations (Schmitt & Pilcher, 2004). For example, if sexual coercion is an adaptation, it needed to be associated with reproductive success. Although current associations with reproductive success are not directly relevant, it may show that sexual coercion could have been associated with fitness in ancestral environments. Gottschall and Gottschall (2003) found that the pregnancy rate from rape was not different from the pregnancy rate from consenting sex, and the pregnancy rate from rape was surprisingly higher after controlling for contraceptives. Given various sources and lines of evidence, the following types may be best explained as an adaptation.

Table 27.1 Evolutionary Typology of Sexual Offenses

	Adaptation	**By-product**	**Disorder**
Obligate	Psychopathy	Sexual homicide	Developmentally disabled; Incest
Facultative-developmentally fixed	Competitively disadvantaged	Sexual homicide	Paraphilias (pedophilia, zoophilia, gerontophilia)
Facultative-developmentally flexible	Young male syndrome; Cuckoldry Risk; Sexual Bullying	Sexual homicide	Paraphilias (exhibitionism, voyeurism, toucherism, frotteurism, frotteurism, biastophilia, necrophilia); Pathological jealousy

THE YOUNG MALE SYNDROME

The *young male syndrome* suggests sexual coercion is more likely to be used by younger men because they are at an age where competition for establishing mateships is highest. Higher fitness variance among males results in higher

competition for mateships, which is why men are more sexually coercive than women (Wilson & Daly, 1985). The costs and benefits of such risky actions changes across the lifespan—as males get older and acquire a mate, the benefits of risky competition no longer outweigh the costs because parental investment becomes a more viable strategy. Lalumière et al. (2005) hypothesized that the young male syndrome is a primary, facultative path to sexual offending, accounting for most sexual assaults against adolescent or adult females.

Much of the empirical literature is consistent with this explanation. Known as the fundamental data of criminology, age and sex are well-known correlates of most crimes, including sexual crimes as well. Moffit and colleagues also discovered what they called "adolescent-limited" offenders as one of two major developmental paths to offending. This group matches what we expect from the young male syndrome—these offenders start committing crimes later in adolescence and desist in early adulthood, and their developmental trajectory also seems typical—they are not characterized by neurocognitive deficits or poor parenting (Moffitt, 2003; Moffitt & Caspi, 2001). Other patterns are also consistent with this explanation: age and sex correlates of sexual crimes are found across time and locations (Lalumière et al., 2005), male hormone levels decrease after marriage (Gettler et al., 2011), some indication marriage is a protective factor for sexual recidivism (Hanson & Bussiere, 1998; Quinsey et al., 1995; Rice et al., 1991), and species with higher variance in male reproductive success (i.e., polygyny), and thus higher levels of competition among males, have males who engage in riskier and sexually coercive behaviors (Lalumière et al., 2005; Wilson & Daly, 1985).

To explain why there is variation in the number of young men who are sexually coercive, Lalumière et al. (2005) suggested that individual differences may result from conditions where the fitness benefits of using aggressive sexual tactics outweigh the costs. For example, having antisocial friends may increase the amount of competition for mateships or may reduce the reputational damage for using a sexually coercive strategy, or being anonymous reduces the costs of being caught, as seen in wartime rape and higher probability of rape by younger men during robberies (Felson & Cundiff, 2012). The young male syndrome is a developmentally flexible path because it addresses a temporary barrier to reproductive success.

Most recently, two studies have found that rape may function to not just increase reproductive success with that victim but to establish longer-term mating relationship with that person. Ellis found that approximately 23 percent of female sexual assault victims had at least one additional instance consensual intercourse after the sexual assault. There were, however, methodological

concerns with this study as it was not clear whether victims had a preexisting sexual relationship with the perpetrator (Camilleri, 2012). Sawatsky et al. (2016) addressed this limitation and found that even after controlling for prior sexual relationships, sexual assault still resulted in a higher chance of consensual sex with the perpetrator after the assault.

Though younger males account for most sexual offenses, there are some sexual offenses that are committed by older men, and some offenders persist throughout their life, and so they require alternative explanations.

COMPETITIVELY DISADVANTAGED

A second major pathway to sexual offending is those considered competitively disadvantaged. Lalumière et al. (2005) described this path as a facultative-fixed pathway—men who experience social and neurological disadvantage early in development become permanently oriented toward a life of risk-taking, antisociality, and mating effort, including sexually coercive behavior. Theoretically, these early experiences signal a future where acquiring mateships will be difficult, due to scarce resources, lower status, or undesirable traits, so an adaptation that facultatively responds to such an environment would benefit men by increasing the probability of engaging in risky behavior to pursue mating. This pathway to offending is hypothesized to be permanent (i.e., facultative—developmentally fixed) because the types of conditions that give rise to competitive disadvantage are not likely to change, especially in ancestral environments where such an adaptation would have evolved, unlike the young male syndrome where its conditions change as people age.

PSYCHOPATHS

Psychopaths are the only path to sexually coercive behaviors that may be obligate. Mealey first proposed that psychopaths may have evolved through frequency dependent selection—that as a cheater strategy, it is only adaptive if it exists as a small proportion of the population. Psychopaths cheat in many contexts, including using sexually coercive actions for mateships. Psychopathy is similar to competitive disadvantage in that both are life-course-persistent offenders, but unlike competitive disadvantage, variation in psychopathy is likely due to variation in genes, not environments. Much of the empirical data is consistent with this theoretical framework. There are parallels in other species, where a subset of males who engage in “sneaker” mating (i.e., nonpreferred males who fertilize eggs by sneaking on the nest or female) are genetically different from males who are preferred as mates, and do not typically resort to sneaker tactics (reviewed in Camilleri & Stiver, 2014; Lalumière et al., 2005).

Behavior genetics research also shows stronger genetic contribution to psychopathy than environment (Burt, 2009; Ferguson, 2010; Viding et al., 2005).

Psychopathy has been implicated in all types of sexually coercive acts, including rape (Porter et al., 2000), partner rape (Camilleri & Quinsey, 2009a), and sexual harassment (Zeigler-Hill et al., 2016) and is one of the strongest predictors of sexual recidivism among incarcerated males (Hawes et al., 2013). Also consistent with this theoretical view is some evidence that showed a positive association between psychopathy and sexual arousal toward coercive sex against adult women (i.e., biastophilia) and negatively associated with sexual arousal toward children (i.e., pedophilia; Harris et al., 2007), and another study found that rapists and rapist/molesters had a higher proportion of psychopaths than child molesters (though psychopathy scores of child molesters were higher than nonoffender controls, and the mixed rapist/molester group had the highest proportion of psychopaths). These data suggest psychopaths' sexual coercion targets reproductively viable women.

It should be noted that although the young male syndrome, competitive disadvantage, and psychopathy are pathways to sexual coercion, they are also used to understand criminality more generally (Quinsey et al., 2004). It seems as though each of these pathways target competition for resources, status, and mateships by increasing mating effort, antisociality (i.e., rule breaking), and risk taking.

SEXUAL BULLYING

Sexual bullying is defined as a relationship problem where an imbalance of power is used to employ sexual acts that are harmful to the other person. Volk et al. (2012) discussed how sexual bullying could be adaptive. Bullies seem to start puberty earlier, interact more with members of the opposite sex, start dating younger, have more dating opportunities, and are more likely to be in a dating relationship. Intersexual bullying may also be a form of sexual coercion by using "pushing and poking" harassment to get a sense of someone's sexual interest. For males, sexual bullying may also be more direct to establish a dating or mating opportunity, or to maintain exclusivity with a mating partner, as seen in men's aggressive response to sexual jealousy. Though Volk and colleagues focused on adolescents, this mechanism can be seen in other ages and contexts, such as sexual harassment in the workplace, when men in supervisory or upper management positions pursue sexual relations with lower-ranked female employees.

CUCKOLDRY RISK

More recently, attention has been given to sexually coercive behaviors in intimate relationships. Sexual conflict theory has been used to understand how cuckoldry risk (i.e., when men who unknowingly raise another man's offspring) is an important contributor to partner rape. Cuckoldry risk is a major source of conflict in committed, intimate relationships. Concealed ovulation makes it impossible for men to be completely sure that offspring are theirs; partner infidelity therefore poses significant costs, and so we might expect that men evolved psychological adaptations to identify and minimize that risk. Sexual coercion in response to partner infidelity minimizes the risk of cuckoldry because it could increase the probability of fertilization by engaging in sperm competition (sperm from more than one male competes for fertilization). Such actions are costly to women because there is a risk of injury and of reduced mating options. After using various methods and populations, cuckoldry risk appears to be a consistent correlate of intimate partner sexual coercion (Camilleri & Quinsey, 2009b; Goetz & Shackelford, 2009, 2006; McKibbin et al., 2011; Starratt et al., 2008). Comparative evidence has also shown that forced copulation in response to potential cuckoldry risk is also found across species that form pair-bonds (Lalumière et al., 2005). Cuckoldry risk appears to function as a developmentally flexible mechanism because only under such higher-risk situations do the reproductive benefits of sexual coercion potentially outweigh the costs.

Sexually Coercive By-products

By-products are traits that are not functional or associated with survival or reproduction but exist as an unintended by-product of another adaptation. Men's rape of reproductively aged women could be a by-product of men's interest in impersonal sex, stronger sexual response to visual stimuli, higher sexual drive, disinterest in abstaining from sex, interest in sexual variety, and less choosiness in mating partners (Palmer, 1991; Symons, 1979). Each of these original adaptations function to increase reproductive success through mate number, all of which makes sexual coercion more likely. There have been a few setbacks with by-product explanations of rape. Initially, Palmer suggested there is little evidence across species that forced copulation is committed by lower-status males, but subsequent work has shown that some species do show this pattern. Also, low-status males are just one of many other possible functions of sexual coercion (see sections "Young Male Syndrome," "Psychopaths," and "Cuckoldry Risk"). Third, sometimes data used to support rape as an adaptation were also used to support rape as a by-product, such as the proportion of rapists who show

sexual arousal to stories depicting coercive sex (see Camilleri, 2012). Fourth, there are very few, if any, direct tests of the by-product hypothesis. Much of the literature that attempts to support the by-product hypothesis does so by attempting to falsify adaptive explanations, yet rigorous tests designed to falsify by-product hypotheses have not yet been published.

There are, however, some sexual offenses that seem to fit the criteria for a by-product. Sexual homicide could not be an adaptation because it does not increase fitness and presents many costs, such as gaining a damaging reputation and having victim family members seek retribution. A likely explanation is that sexual homicides are a by-product of adaptive pathways to sexual offenses that have gone awry, such as worry that the victim would pursue charges, the victim fighting back, or the perpetrator being under the influence of substances. Order of offending behavior is important here because homicide followed by sexual assault (i.e., necrophilia) is likely a disorder. Sexual homicides are complicated to understand because each behavior could even result from independent mechanisms—either action could result by some combination of by-products and/or adaptations (e.g., adaptation to rape and adaptation to conceal crime).

Sexually Coercive Disorders

Wakefield (1992) provided a useful framework for understanding psychological disorders by using the concept of "harmful dysfunction"—psychological disorders from an evolutionary framework require two conditions that must be met for a disorder: (1) mechanism is not functioning in the way it was designed and (2) the malfunctioning mechanism is harmful. The second condition is satisfied by the fact that all sexual crimes are harmful to the victim, so much of the attention needs to be on identifying which mechanisms are malfunctioning. Paraphilias, incest, developmentally disabled sexual offending, and pathological jealousy are types of sexual coercion that meet these criteria.

PARAPHILIAS

Some paraphilias meet the criteria for a disorder if the person acts on them. For example, pedophilia is hypothesized to result from malfunctioning mechanisms that men use to detect sexual maturity from body shape (Quinsey & Lalumière, 1995). Evidence consistent with this explanation is that pedophilia is associated with factors that impact development or are markers of atypical development, such as lower IQ (Cantor et al., 2004), head injury before the age of thirteen (Blanchard et al., 2003), and fraternal birth order effect (Lalumière et al., 1998).

Some attention has been given to voyeurism, exhibitionism, and toucherism, suggesting they result from a courtship disorder, where the paraphilia represents an exaggerated act of courtship. Voyeurism is a disorder of interest in viewing potential mates, exhibition is a disorder of pretactile interaction, and toucherism is a disorder of tactile interaction. Though consistent with Wakefield's concept of harmful dysfunction, there are some problems with Freund et al.'s hypothesis. Because many of these paraphilias are comorbid, they could not result from a disorder of a specific courtship phase. We need a stronger grasp on phases of courtship before testing whether its disruption could lead to certain paraphilias. For instance, do men and women differ on these courtship phases? Since men disproportionately exhibit paraphilias (reviewed in Dawson et al., 2016), any explanation of the disorder would need to address this sex difference.

Other paraphilias may result from disordered adaptations. A plausible malfunctioning mechanism could be age for gerontophilia, or mechanisms that make interspecies mating aversive or conspecific mating desirable are malfunctioning among zoophilia. Other paraphilias may result from malfunctioning mechanisms associated with adaptive functioning of sexual coercion. For example, the mechanism that allows for arousal to consenting situations may be disrupted in biastophilia or necrophilia. These hypotheses have yet to be fully developed and tested.

INCEST

Genetic father incest has been hypothesized to result from a disordered incest avoidance mechanism (Seto et al., 1999), and it may also occur more frequently when paternity uncertainty is higher. Incest avoidance may not always be an optimal strategy and in some cases may be unnecessary or costly. Some mathematical models have suggested that in some species, incest avoidance varies between the sexes or depend on particular conditions (e.g., Haig, 1999; Kokko & Ots, 2006; Welham, 1990). Though these evolutionary-informed hypotheses have some empirical support, more direct tests, particularly among humans, are needed.

DEVELOPMENTALLY DISABLED

Two hypotheses have been proposed about the association between developmental disability and sexual offending: (1) the disability represents an extreme form of competitive disadvantage, and so it functions as an adaptive response to limited mateships or (2) the disability impacts the execution of various mechanisms (Camilleri & Quinsey, 2011). The data appear to support the latter, as lower IQ is associated with more deviant sexual arousal patterns,

including arousal toward children, and victims of developmentally disabled sexual offenders are more likely to be prepubescent. It is not clear which specific mechanisms are impacted, but research on impaired processing of cost-benefits associated with sexual coercion is a likely explanation.

PATHOLOGICAL JEALOUSY

Pathological jealousy (sometimes referred to as delusional jealousy, Othello syndrome, morbid jealousy, and conjugal paranoia) appears to be a disorder of sexual jealousy. Jealousy is an emotional response to someone impacting a valued interpersonal relationship and is a functional response because it motivates the person to reduce the negative impact of that person. Sometimes these mechanisms malfunction and people persistently believe a threat to one's relationship exists when one does not, even after being presented with evidence (Kingham & Gordon 2004). Since men are more prone to experiencing sexual jealousy because cuckoldry risk is very costly, and women are more prone to experiencing emotional jealousy because losing resources to a rival would be costly, we would expect similar sex differences in their pathologies. Easton et al. (2007) found that indeed men with morbid jealousy were more prone to sexual jealousy, and women with morbid jealousy were more prone to emotional jealousy.

Determining when jealousy amounts to pathology is difficult, given that jealousy could function as an adaptive error as predicted from error management theory (Buss & Abrams, 2017). From this theoretical model, it may be adaptive for men to err on the side of incorrectly thinking their partner is cheating on them, because it would have been less costly than incorrectly thinking their partner has been sexually faithful. Interestingly, many cases of pathological jealousy resulted in men finding out their partner was indeed having an affair (Buss, 2000).

Summary and Future Work

Darwin's seminal idea that complex biological traits evolve through natural and sexual selection fundamentally changed the way we understand the natural world. Its application to human psychology and behavior, though controversial, had an equally important impact because for the first time, psychology had a theory that could unite its subdisciplines and bridge the gap between human and nonhuman scientific literatures. Sexual selection, a middle-level theory on sexual conflict, has been prolific in understanding many sex differences in traits and behaviors and has been integral in understanding sexual coercion.

Unity and fecundity are hallmarks of a good theory, and as this review has shown, Darwin's theory of sexual selection satisfied both by integrating knowledge and findings across disciplines and providing an overarching framework to explain the etiology and variety of sexual coercion. Its application to human sexual coercion has been slower than the work on sexual coercion with nonhumans. Academic resistance is likely due to a misunderstanding of evolutionary psychological principles and perceived threats of a paradigm shift. Though more empirical work is still needed to get a better grasp of evolutionary impact on sexual coercion in humans, we have a typology that provides a framework to account for variation in sexually coercive behaviors. Stronger ties to applied areas in criminal justice are also needed, particularly in understanding risk factors, offenders' receptivity to treatment, and identifying specifically which psychological factors should be targeted. For example, the developmental trajectories of sexual offenders have implications on how best to intervene: *Facultative-fixed* requires primary or secondary prevention, whereas *facultative-flexible* can be addressed through tertiary prevention as well.

Admittedly, evolutionary approaches to sexual coercion among humans is not without controversy. One of the more popular positions used to argue against the validity of this approach is really about the implications—that if sexual coercion is a product of evolution, then it justifies men's use of it. Concern about how wider audiences may use such information to justify sexually coercive actions are legitimate and must be addressed. Here we have a salient example of the *naturalistic fallacy*—believing that just because something *is* a certain way means it *ought* to be that way. There are many problems with the naturalistic fallacy. First, evolutionary approaches explain why sexual coercion exists, but such explanations have no bearing on whether an act is "right" or "wrong". Viral strains are harmful, and yet we study them from a selection process with no controversy—no one argues that viruses are justified in their harm. But understanding virus etiology, composition, function, mutations, and so on, helps us find ways to prevent its spread or alleviate its impact. Second, although evolution may have selected mechanisms for specific motivations, people still have the cognitive capacity and responsibility of deciding whether to act on them or not—culpability therefore resides solely within the person. As reviewed in this chapter, these fears may have prevented scholarly activity on sexual coercion since first applying them to humans more than forty years ago. Misuse or misinterpretation of scientific theory and findings is no reason to suggest evolution cannot explain sexual coercion. It is our responsibility to more thoroughly and adequately communicate science to a wider audience, and given the sensitivity of the topic, researchers must adhere to the highest standards of

scientific rigor and criticism.

As reviewed in this chapter, evolutionary models have significantly improved our ability to explain patterns in sexual coercion observed *between* and *within* species, sexes, and circumstances. These patterns include variation in frequency, severity, type (e.g., partner rape and child molestation), and etiology (i.e., adaptation and by-product, disorder). Not only has this approach given psychology a framework to understand human behavior in the same way behavioral ecologists understand nonhuman behavior, which allows for greater transmission of ideas, it also provides necessary theoretical connections between psychology's subdisciplines, such as behaviorism, neuropsychology, cognition, social, and development. Over time, academics outside the natural sciences have become more receptive, and even inclusive of Darwinian principles, yet some well-intentioned works continue to promote inaccurate evolutionary models, as is seen in integrated models of rape, suggesting more rigorous review and criticism of these works are needed. Promising new lines of evolutionary-informed research on sexual coercion include studying women's evolved defenses against it (see Chapter 28, this volume), developing clinical and programmatic interventions to reduce its prevalence, refining and testing components of the sexual offending typology, and pursuing recent middle-level theoretical developments on sexual coercion, such as sexual conflict theory and error management theory. Remarkably, Darwin's 150-year-old idea of sexual selection drove substantial theoretical and empirical progress on understanding sexual coercion and continues to inspire research ingenuity on such a widespread and dangerous behavior.

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Note

1. Younger female victims is also consistent with a more general rape adaptation and with the rape as by-product hypothesis (i.e., by-product of men's attraction to younger women).

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CHAPTER
28

Women's Avoidance of Sexual Assault

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Abstract

Men's sexual aggression against women has been a recurrent feature of human evolutionary history. Most of the research in this area has focused on why men are perpetrators of sexual assault, and why women are victims of sexual assault. However, given the reproductive costs of sexual victimization for women, it is important to also examine whether women are equipped with a psychological architecture that operates to avoid or thwart sexual assault. In this chapter, we discuss women's psychology of rape avoidance using the framework of an evolved threat management system. The system is proposed to include an emotional calibration system that operates in response to variables that increase the risk or costs of sexual victimization. Women who are disproportionately at risk of becoming the victim of sexual assault, or for whom such threats would be particularly costly, are expected to experience a calibrated fear response. It is this fear that motivates adaptive behavioral adjustment to avoid or thwart sexual assault. This includes manifest behaviors deployed to defend against sexual aggression, including not walking alone at night and being more attuned to one's surroundings. We review the extant research on the association between factors that increase the risk and costs of sexual victimization and the emotional and behavioral output that fosters avoidance of sexual threats.

Key Words: sexual aggression, avoidance of sexual aggression, sexual threat, risk of sexual victimization

Prevalence of Sexual Aggression Sexual assault[1] is a widespread social, health, and economic issue that is associated with many negative outcomes for victims, including worsened psychological and physical health (Romito & Grassi, 2007). Much research on sexual aggression has focused on the prevalence of men's perpetration of sexual violence against women and women's experiences of sexual victimization, indicating men are typically the perpetrators of sexual assault (Morgan & Oudekerk, 2019) and women are typically the victims of sexual aggression (National Sexual Violence Resource Center, 2011). Men's sexual aggression is common; a recent meta-analysis examining seventy-eight independent samples of college-age men (N = 25,542) found that 29 percent of men report engaging in sexual perpetration behaviors, with an average of 19 percent engaging in verbal coercion and 6.5 percent engaging in rape (Anderson et al., 2021). Approximately 0.05 percent to 8.4 percent of college-age women report having been the victim of sexual assault (Fedina et al., 2018), with higher estimates suggesting that approximately 25 percent of college-age women have been the victim of at least one attempted or completed rape (Cantor et al., 2015). In another study featuring a more inclusive age sample (fifteen to seventy years), researchers found that 54 percent of women have experienced at least one type of sexual violence (de Haas et al., 2012). Sexual victimization is associated with many adverse consequences, such as greater depression, anxiety, and reduced self-perceived value, particularly among women (Perilloux et al., 2012; Romito & Grassi, 2007). Given the pervasiveness and outcomes of sexual violence, it is important for researchers to investigate its causes and consequences.

Although other psychological perspectives are often utilized in investigating women's rape avoidance behavior, an evolutionary psychological perspective is particularly informative, given the immense reproductive costs that sexual violence exacts upon women (Thornhill & Palmer, 2001; Trivers, 1972). In this chapter, we first discuss evidence consistent with the argument that women evolved psychological counteradaptations to mitigate the recurrent threat of rape and the reproductive costs associated with victimization. We then argue that women are likely equipped with a suite of psychological mechanisms for managing and mitigating the threat of rape, taking the form of a psychological threat management system for rape avoidance (McDonald et al., 2015; Neuberg et al., 2011). In support of this perspective, we review the extant literature on perceptual cues that motivate activation of such a psychological system, as well as the subsequent emotions and behaviors that function to avoid or thwart sexual threats. In particular, we focus on defenses women may have evolved to thwart rape attempts from strangers and acquaintances, as defensive strategies to

mitigate partner rape likely require a different behavioral strategy. Importantly, our review of the research on a threat-management system for rape avoidance is not intended to suggest that the burden of reducing sexual violence is the responsibility of women. The responsibility for rape rests with the perpetrator, regardless of the strategies that women may, or may not, use to protect themselves from sexual assault.

The Costs of Rape

To make an argument that women possess a specialized psychological system for rape avoidance, at least two conditions must be met. First, rape must have been a recurrent threat to women in the ancestral *environment of evolutionary adaptedness* (EEA; Hagen & Symons, 2007). Second, rape must have exacted costs on women's reproductive fitness. Accordingly, there is much evidence that sexual violence was a pervasive and recurrent threat for ancestral women. In a review of anthropological studies that examined primitive societies that are argued to reflect ancestral life in the EEA, the occurrence of rape was universal across societies and its presence could not be explained by culture (Palmer, 1989). In another investigation that assessed a random sample of thirty-five nonindustrial world societies, the concept of rape was universally present, regardless of cultural acceptance (Rozée, 1993), providing evidence that sexual aggression may be a fundamental feature of human societies, persisting even when socially sanctioned.

More evidence for a recurrent threat of sexual aggression against women throughout history can be found in ancient literary works. Ancient Greek and Roman mythologies (estimated to have originated around the eighteenth and eighth centuries bc, respectively) feature passages about sexual violence directed toward outgroup women during times of intergroup conflict. The Greek epic the *Iliad* (Homer, 1998) includes the story of a young woman who is raped by an enemy leader after the fall of Troy, and Roman mythology contains a story about a strategic Roman abduction of Sabine women who were to be used as child bearers (Livius, 1912). Despite being fictional in nature, such literary narratives may provide important reflections of the lives of the individuals who lived during these periods and those who lived before them, presenting circumstantial evidence for the threat of wartime rape among human ancestors. Evidence for recurrent sexual violence against women is also found in earlier historical records of criminal laws, which were established to prevent individuals from engaging in behavior they otherwise might without such legal sanctions. For example, the Babylonian's Code of Hammurabi contained the earliest recorded

rape law, written approximately four thousand years ago in 1900 bc (Gold & Wyatt, 1977). The code was limited, however, to prohibiting rape of women already betrothed, thereby permitting rape in other contexts. Such records suggest that sexual violence was widespread and disruptive enough to garner the attention of ancient lawmakers.

According to Triver's (1972) parental investment theory, men and women provide differential levels of parental investment in offspring. Women, relative to men, bear larger physical and biological costs of childrearing (e.g., a long gestational period, lactation, and limited gamete production), thereby constraining the total number of offspring women can conceive in a lifetime. For men, all that is required is an ejaculation, resulting in a nearly limitless reproductive ceiling. From this perspective, men are more likely to pursue a short-term sexual strategy, whereas women are more likely to pursue a long-term sexual strategy, of which a key feature is reproductive choice (Buss & Schmitt, 1993). Women's choosiness in selecting a mate functions to ensure the reproductive success of their limited number of offspring by selecting high-quality men who can provide support and resources to themselves and their offspring (Buss 1989; Trivers, 1972). This produces intersexual competition, under which men are motivated to gain access to many mating opportunities and women are inclined to discriminate against all but the most appealing male partners (Buss, 1989; Buss & Schmitt, 1993).

In response to this intersexual competition, researchers suggest that men's proclivity for sexual aggression may be an adaptive, albeit exploitative, facet of men's short-term mating strategy (Apostolou, 2013; McKibbin et al., 2008; Thornhill & Palmer, 2001). Although research is not settled on whether men's rape psychology is an evolutionary by-product or a direct product of adaptive selection, men's sexual aggression is most likely to occur in contexts where the likelihood of success is high and the risk of detection and repercussions is low (Gottschall, 2004). There is ample evidence across disciplines that indicate that intergroup warfare has been a recurrent feature throughout human evolutionary history (Glowacki et al., 2017; Pinker, 2012; Sugiyama et al., 2018; Van Vugt & Park, 2009). Frequent intergroup warfare provided conditions for men's sexual aggression owing to a high likelihood of success and a low risk of consequences (Keeley, 1996; Sanday, 1981; Wrangham & Glowacki, 2012; Wrangham & Peterson, 1996). For example, Gat (2000) and Sanday (1981) found that modern hunter–gatherer intertribal warfare, thought to be similar to warfare occurring in the EEA, is associated with sexual violence toward outgroup women. Thus, women were likely to have faced a recurrent and pervasive threat of sexual aggression throughout evolutionary history.

Due to high parental investment and the importance of reproductive choice among women, sexual victimization is extremely reproductively costly to women, creating selection pressure for counteradaptations that reduce the risk or costs of being victimized. The circumvention of female sexual choice via rape negatively impacts women's reproductive fitness, as women may be coerced to biologically invest in the offspring of an undesirable male who has little incentive to provide resources to the family. Moreover, female rape victims also risk losing the paternal investment of a current partner (McKibbin et al., 2008; Symons, 1979). For example, in the context of wartime rape among primitive societies, conquered groups' women are regularly raped and coerced into marriages by rival men (Gat, 2000), directly thwarting women's reproductive choice and dissolving established partnerships that likely procured fitness-enhancing resources. If such societies are reflective of the EEA, the evidence suggests that it would have been adaptive for women to evolve counteradaptations to reduce such reproductive costs.

The necessity for counteradaptations to avoid the reproductive consequences of rape is exacerbated by some, albeit limited, evidence suggesting that the likelihood of conception is greater following rape as compared to consensual sex. A review of US sexual victimization data between 2010 and 2012 found that 2.4 percent of women report a pregnancy from rape at some point in their lives (Basile et al., 2018). Additional research has shown that, among reproductive-aged women (fifteen to forty-five years), 6.4 percent of women who were raped became pregnant, whereas incidence of pregnancy among reproductive-aged women in the general population was 3.1 percent (Gottschall & Gottschall, 2003). Work from the Netherlands suggests that of female rape victims, approximately 7 percent became pregnant as the result of rape (de Haas et al., 2012). However, without a precise control for victim age, these results may be explained by the disproportionate number of young women rape victims (Felson & Cundiff, 2014 Sinozich & Langton, 2014; Thornhill & Thornhill, 1983) who have greater reproductive fecundity in general (Dunson et al., 2002). Although more research is needed to clarify these findings, it is likely that rape presents as great a risk of conception as consensual sex, if not higher.

Sexual aggression exacts many other reproductive costs, aside from limiting female sexual choice. In line with parental investment theory that emphasizes the distinct importance of women's biological investment in offspring (Trivers, 1972), the threat of physical violence that is often associated with sexual aggression may reduce women's reproductive fitness, particularly among those of reproductive age. Because women invest more biological resources in offspring, women's ability to care for existing offspring, and their ability to bear

future offspring, may be especially harmed by physical violence during rape. Using a national sample of women, Chen and Ullman (2010) found that, 41 percent of women perceived life threat during sexual assault, 33 percent of sexual perpetrators used physical force against the victim, and 27 percent of women experienced some form of physical injury owing to sexual assault. Such evidence suggests that concurrent physical and sexual assault threatens women's fitness, with physical injury likely impacting women's ability to care for existing offspring. Additionally, researchers have described other social and psychological consequences of rape that may influence the reproductive costs exacted upon sexually victimized women. For example, the inability to optimally time pregnancies (Thornhill & Palmer, 2001), as well as a tarnished sexual reputation and reduced sexual desire—both of which are common outcomes reported by female victims, particularly among women who experienced a *completed* assault as opposed to an attempted one (Perilloux et al., 2012). Given the depth of work documenting sexual violence as commonplace throughout human evolutionary history and the immense reproductive costs that rape exacts upon women (e.g., circumvention of sexual choice), women likely evolved counteradaptations to mitigate the threat and costs of sexual victimization.

Women's Counteradaptations to Rape

Cross-species comparative work on the coevolution of rape and rape avoidance may be helpful in understanding human behavior, due to similar challenges of intersexual conflict. Research suggests that females of other species, who have faced recurrent threat of rape or forced mating, have coevolved adaptations to thwart the reproductive costs of rape (Crawford & Galdikas, 1986). For example, the morphology of genitalia in ducks suggests that males and females have engaged in intersexual conflict over evolutionary time, due to the immense threat of rape by males (Brennan et al., 2010). Specifically, female waterfowl have coevolved, in response to male sexual aggression, counterclockwise corkscrew (e.g., spiral-shaped) vaginas, which make phallic insertion more difficult (Brennan et al., 2010). In orangutans, a more closely related species to humans, females engage in fierce physical defense behaviors (e.g., biting and hitting) when targeted for forced copulation by nonconsort males (Galdikas, 1981; Stumpf et al., 2011). Knot et al. (2010) observe that female orangutans, however, are rarely physically wounded during such attempts, as males do not engage in physical aggression, instead focusing primarily on preventing female escape. As such, female orangutans' physically defensive rape avoidance strategies may be effective due to a low risk of

physical retaliation by males.

Human evidence suggests that women also use physical retaliation to escape sexual attacks. Women's physical resistance against sexual violence, including fighting, fleeing, and yelling, reliably reduces the likelihood that they will become the victim of a completed rape (Hollander, 2018; Ullman, 2007; Quinsey & Upfold, 1985). However, considering sexual dimorphic characteristics in humans, such as strength and size differences between men and women, women are at a physical disadvantage for fending off violent attacks by men (Sell et al., 2012). Not only are women, on average, less physically formidable than men, but because women's reproductive capacity relies heavily on biological investment in offspring, threat of bodily harm should be avoided whenever possible (Campbell, 2013). As such, pure reliance on physical defense against sexual attackers may negatively impact women's reproductive success. Therefore, it may be most adaptive for women to mitigate sexual fitness threats *before* they occur.

A Psychological Threat Management System for Rape Avoidance

Given the recurrent threat of sexual aggression faced by women throughout evolutionary history, in combination with the severe reproductive fitness costs posed by sexual assault, women may have evolved a precautionary *threat management system (TMS) for rape avoidance* (Neuberg et al., 2011). Such a system would function to monitor the risk and costs of sexual assault and, in response, motivate defensive vigilance behavior to avoid sexual victimization. Neuberg et al. (2011) suggests that TMSs are self-protective precautionary fixtures of human psychology that evolved to respond to, and mitigate, adaptive threats that were recurrent in the EEA. For example, humans may have evolved a TMS for disease avoidance, as disease was a frequent adaptive challenge throughout human evolutionary history. In response to perceptual, or sensory, cues that signal disease, humans experience strong disgust reactions that motivate avoidance of the target, thereby increasing one's survival and reproductive prospects (Neuberg et al., 2011; Oaten et al., 2009). Such self-protective psychological systems are responsive to individual characteristics that may make certain individuals more or less vulnerable to those threats, as well as perceptual cues of threat from one's environment, such as interacting with strangers who may possess novel pathogens in the case of a disease avoidance TMS (Oaten et al., 2009). Neuberg et al. (2011) suggest that in response to cues of threat, TMSs are expected to activate, or produce, emotions and cognitions that motivate behavioral responses that function to reduce threats to reproductive

fitness. Threat-specific cues act as inputs for specialized TMSs, subsequently producing emotional and cognitive responses that prompt adaptive behavioral output.

A precautionary TMS for rape avoidance should activate in response to cues, or inputs, that convey an increased risk of being the target of sexual assault (e.g., women who are reproductive-aged), as well as to inputs that signal greater reproductive costs of being victimized (e.g., women who are at increased conception risk; McDonald et al., 2015). In other words, women who are at an increased likelihood of sexual victimization, or at risk of greater reproductive costs if victimized, are expected to experience TMS activation that generates a fearful emotional response that is calibrated according to the degree of threat. Fear is the expected emotional output of a TMS for rape avoidance because threats to physical and/or sexual safety are expected to produce an emotional response that motivates escape behavior to increase the likelihood of survival (Neuberg et al., 2011). As such, one's degree of rape fear should motivate symmetrically severe behavioral responses that function to avoid or thwart sexual attacks, such as avoiding dark, scarcely populated areas alone (McDonald et al., 2015).

Inputs for a TMS for Rape Avoidance

For a TMS for rape avoidance to motivate adaptive behavior, perceptual cues that signal greater sexual threat and reproductive cost must, consciously or unconsciously, be input into the system. We argue that such a system in women is expected to be responsive to inputs such as (1) the likelihood of being targeted and (2) the reproductive costs of being targeted.

LIKELIHOOD OF BEING TARGETED

There are many individual differences among women that may contribute to a greater likelihood of being targeted for sexual aggression, including age, mate value, possessing characteristics that are perceived as sexually exploitable by men, dangerousness of local environment, and proximity of kin. Such individual and situational variability should therefore act as inputs to a TMS for rape avoidance.

Research demonstrates that men prefer young and attractive women for both short- and long-term mating, likely owing to increased fertility and reproductive value, or greater time available for future reproduction among younger women (Buss, 1989; Buss & Schmitt, 1993). Biological work on female reproduction substantiates such claims, as women's fertility peaks in their twenties and begins

to decline in their thirties (Dunson et al., 2002; Gruhn et al., 2019). As such, men's preference for reproductive-aged women likely guides their sexually aggressive behavior (McKibbin et al., 2008; Thornhill & Palmer, 2001). However, it is possible that young women are preferentially targeted for sexual assault owing to their greater exploitability, not their fertility, but the fact that men prefer younger women for consensual short- and long-term dating suggests that it is not likely to be exclusively based in susceptibility to exploitation. Regardless of the motivation, there is robust evidence that women under the age of thirty-five are the primary targets of sexual assault (Centers for Disease Control and Prevention, 2015; Chen & Ullman, 2010; Felson & Cundiff, 2014; Sinozich & Langton, 2014). Accordingly, reproductive-aged women should be especially sensitive to rape threat because younger women are at increased risk of being victimized.

The association between women's mate value, or physical attractiveness, and sexual assault is not as clear, as there is very little research that separates the influence of age from physical attractiveness. However, in one particularly relevant study, fourteen- to sixteen-year-old girls who indicated they were higher in physical attractiveness were 3.6 times more likely to report sexual victimization than those with lower attractiveness scores (Savolainen et al., 2020). In qualitative interviews with serial rapists, researchers found that 38 percent reported that they targeted victims based on physical appearance and 7 percent reported that they targeted victims based on sexual appearance, though the distinction between the two factors is ambiguous (Beauregard et al., 2007). As a result, evidence is limited to suggest that physically attractive women are sexually targeted more often than unattractive women of the same age. It may be the case that serial rapists would prefer to select sexually attractive victims, but that other factors, such as accessibility and exploitability, outweigh that preference as a means of reducing the risk of getting caught.

Along these lines, evidence suggests that men are attracted to cues of women's sexual exploitability (Goetz et al., 2012). Indeed, men are attuned to a variety of women's behavioral and psychological cues of exploitability, such as style of gait (Sakaguchi & Hasegawa, 2006), being the under influence of alcohol (Untied et al., 2013), and immaturity and low self-esteem (Goetz et al., 2012). Interestingly, evidence suggests that women are likely aware, whether consciously or unconsciously, that men find such traits sexually appealing. Goetz et al. (2014) report that women who are lower in openness and less oriented toward a short-term sociosexual orientation displayed fewer cues of exploitability, such as immaturity and shyness, in video dating profiles. Such findings suggest that women can discern which traits make them appear more

sexually exploitable and adjust their behavior accordingly. Varying situational contexts, such as consuming alcohol, may also increase an individual's risk of assault, owing to reduced cognitive and physical abilities to resist sexual attacks (Untied et al., 2013). Alcohol consumption increases the likelihood of sexual victimization, as research suggests that intoxication of a perpetrator and/or victim is highly associated with rape (Untied et al., 2013). In a set of qualitative interviews with young women (ages eighteen to twenty-four), Brooks (2008) suggests that women are aware of the sexual dangers surrounding public intoxication, acknowledging that they have reduced ability to maintain defensive vigilance toward threats to their safety while consuming alcohol. Aware of such dangers, most interviewees incorporated strategies to reduce the likelihood of being targeted while drinking at bars or clubs, such as limiting alcohol consumption and seeking protection from male friends (Brooks, 2008). Environments where others consume alcohol (e.g., bars) are therefore likely to activate the TMS for rape avoidance. However, as alcohol consumption increases, women's decision-making processes likely deteriorate.

Women who reside in dangerous neighborhoods may be at increased risk of sexual assault. According to national reports, more than 50 percent of sexual crimes occur in urban regions, as opposed to rural areas that account for 10 percent of sexual crime (Office for Victims of Crime, 2017). Additionally, serial rapists reported that the most important component of victim selection was target location, explicitly indicating that those who reside in low socioeconomic neighborhoods were better targets (Beauregard et al., 2007). A TMS for rape avoidance should therefore be attuned to cues that signal dangerousness of the local environment, particularly when living in lower socioeconomic status neighborhoods or urban areas. Similarly, women who reside in closer proximity to friends and family may be at *reduced* risk of sexual coercion, due to protection from would-be rapists by coalitional allies (Figueredo et al., 2001; Smuts, 1992). The likelihood and costs of retaliation to the perpetrator are likely greater when women are protected by proximal kin. Male friends may also mitigate the threat of sexual attacks by other men; as such, women should be sensitive to the proximity of friends and family.

REPRODUCTIVE COSTS OF BEING TARGETED

A TMS for rape avoidance should be sensitive to information that signals that the costs of sexual victimization are especially high. Women who are assaulted face the loss of their reproductive choice, damage to their physical health and sexual reputation, and a loss of their ability to optimally time pregnancies. Here, we discuss additional reproductive costs that vary among targeted women, such

as the likelihood of conception and the risk of partner defection.

The reproductive costs of being raped are greatest if the rape results in pregnancy. The likelihood of becoming pregnant fluctuates across the menstrual cycle with the greatest risk of pregnancy occurring in the days preceding ovulation (Dunson et al., 2002). Ovulatory windows are therefore associated with the greatest potential costs of sexual assault owing to increased conception risk. Among orangutans, females are more resistant to lower-quality male forced-copulation attempts during ovulatory periods, suggesting that conception risk promotes rape avoidance behavior in another concealed-ovulation primate species (Knott et al., 2010). Evidence suggests that men may be attuned to cues of fertility and conception risk in women, given men's preference for reproductive-aged women (Buss, 1989) and the increased likelihood of pregnancy among rape victims (Gottschall & Gottschall, 2003). These findings suggest that it would be adaptive for women to be especially cautious to avoid sexual aggression during times of high fertility and peak conception risk, as the reproductive consequences of rape are heightened at this time. Consistent with this, research has demonstrated that women display heightened defensive vigilance against sexual threat as a function of elevated conception risk (Bröder & Hohmann, 2003; Chavanne & Gallup, 1998; Garver-Apgar et al., 2007; Petralia & Gallup, 2002). Additionally, because ancestral women faced a recurrent threat of intergroup sexual violence by outgroup males during warfare (e.g., Gat, 2000), women at higher levels of conception risk also express greater bias against outgroup men, an effect that is argued to serve the function of promoting greater vigilance against threats to one's reproductive choice (McDonald et al., 2011; McDonald et al., 2019; McDonald et al., 2015; Navarrete et al., 2009).

Women's sexual victimization may also be associated with partner abandonment because of a perceived risk of infidelity and cuckoldry (Thornhill & Thornhill 1990). Partner defection is reproductively costly to women, because women and their offspring may lose paternal support and resource allocation from their partner. Additionally, research suggests that men's perception of partner infidelity is associated with greater rates of intimate partner violence (Goetz et al., 2008). As noted previously, women should be especially sensitive to physical threat because they invest more biological resources in offspring and provide greater childcare (Campbell, 2013). Therefore, mated women, particularly those who already have children, may be more sensitive to the threat of rape, in order to protect the allocation of resources and support from their partner and to reduce the likelihood of being the target of intimate partner violence.

Emotional Output of a TMS for Rape Avoidance

We argue that fear of rape (FOR) is likely the adaptive emotional response to inputs that signal increased risk of sexual victimization or greater reproductive costs of being victimized. In support of FOR being the emotional response of a TMS for rape avoidance, research suggests that factors that signal increased risks and reproductive costs of sexual assault are associated with greater FOR. For example, research indicates that high perceived likelihood of being raped was the greatest predictor of FOR, particularly in young women (O'Donovan et al., 2007). Research suggests that compared to older women, younger, reproductive-aged women are more fearful of rape, particularly among those who live in more dangerous environments (Warr, 1985). For instance, Warr (1985) reported that young women residing in urban areas believed they had high likelihood of being targeted for rape, indicating that their risk of rape was roughly three times higher than other types of crimes. Such work suggests that women are attuned to perceptual cues that signal greater rape threat and that these cues motivate a FOR response.

Similarly, researchers found that, in interviews with women who served in Iraq and/or Afghanistan, 44 percent reported both fear of being assaulted *and* engaging in preventive behaviors to avoid assault during deployment, given high rates of rape in the military (Weitz, 2015). Among women who felt unsupported during their deployments (e.g., when trusted men and women in their units were not nearby to offer physical protection), feelings of sexual vulnerability were especially high (Weitz, 2015, 2016). Weitz (2015) also reported that situational contexts that confer increased physical vulnerability, such as those that include alcohol consumption, were associated with greater FOR among military women. Together, these findings suggest that sexually dangerous environments, such as military deployment and lack of support and protection from others influences women's FOR.

Investigating conception risk and FOR, one study found that high self-reported mate value positively predicted women's FOR, particularly among women at high conception risk, suggesting that conception risk is an important moderator of women's FOR response (McDonald et al., 2019). Interestingly, concerning relationship status and FOR, researchers have found that *single* women, as opposed to mated women, report greater FOR (O'Donovan et al., 2007). It's possible, however, that these findings are due to a lack of male protection for single women. As such, absence of partner protection may serve as a stronger TMS input than partner abandonment. Overall, these findings speak to the likelihood that women possess a TMS for rape avoidance, as evidence

indicates that there are significant positive associations between cues that signal greater rape threat and FOR.

Behavioral Output of a TMS for Rape Avoidance

Adaptive behavioral outputs of a TMS for rape avoidance should be motivated in response to inputs that evoke rape fear. Rape avoidance behavior, such as avoiding walking alone, avoiding alcohol consumption, and being vigilant of one's surroundings, represent a few of many individual behaviors that women use to mitigate rape threat when feeling afraid (McKibbin et al., 2011). For example, Smuts (1992) suggested that forming protective alliances would have been adaptive for ancestral women because of a reduced likelihood of assault. As such, women may be motivated by FOR to form partnerships, in part, for physical protection. Indeed, researchers have found support for the bodyguard hypothesis that suggests that women's preference for mates who are physically and socially dominant may be a feature of an evolved antirape mechanism that is most active when the risk of sexual assault is especially high (Buss & Schmitt, 1993; Wilson & Mesnick, 1997). Similar evidence emerges in other primates. Female orangutans overwhelmingly prefer larger, dominant males and seek their companionship discriminately (Stumpf et al., 2011), as these males guard and defend females from smaller, undesirable males who often engage in forced copulation attempts (Galdikas, 1981). Researchers suggest that human women prefer physically strong men, particularly in a short-term mating context when threat of assault from other males is high (Buss & Schmitt, 1993). The "sexy sons hypothesis" suggests that women have a preference for attractive men because reproducing with such men would ensure the attractiveness of male offspring, likely increasing gene propagation in the next generation (Smith, 1984). However, because men's physical strength also likely cues protective ability, it is possible that women prefer formidable males for those benefits as well. Similarly, women prefer physical strength in opposite-sex friends, possibly for increased protection from sexual attacks (Lewis et al., 2011). Indeed, research has found that among women, physical protection is an important motivation for initiating opposite-sex friendships, with women reporting that lack of protection by male friends is an important reason for terminating such friendships (Bleske & Buss, 2000; Bleske-Rechek & Buss, 2001). In sum, women's preference for strong, formidable mates may be an output of a TMS for rape avoidance.

Research suggests that kin proximity is associated with rape avoidance behavior. McKibbin et al. (2011) found that the number of nearby kin

(particularly male kin) was positively associated with women's rape avoidance behaviors. However, the directionality of this effect is unclear. Women who are closer to male kin may perform more avoidance behaviors because of their close proximity; alternatively, women with greater FOR may maintain closer proximity to kin, suggesting that living near kin *is* a rape avoidance behavior due to their FOR, rather than a cause of the avoidance behavior (Snyder & Fessler, 2013b).

Women who self-report greater physical attractiveness indicate that they perform more rape avoidance behaviors than women who report lower attractiveness (McKibbin et al., 2011). Snyder and Fessler (2013b) proposed that the relationship between self-perceived attractiveness and avoidance behaviors could be explained by learning because younger women are simultaneously more attractive and more likely to be targeted. Although learning is likely an adaptive behavior that women engage in to reduce their risk of sexual assault (e.g., learning that they live in a dangerous environment and are at greater risk of victimization), some findings suggest that certain sexual threat cues go beyond the scope of conscious awareness. For example, evidence suggests that the association between mate value and FOR is moderated by conception risk (McDonald et al., 2019) and that women engage in greater defensive vigilance to mitigate the threat and costs of rape at heightened conception risk (Bröder & Hohmann, 2003; Garver-Apgar et al., 2007; McDonald et al., 2011; McDonald et al., 2015). For example, women who were closer to ovulation perceived men who were trying to attract women as more sexually coercive than women further from ovulation (Garver-Apgar et al., 2007). Additionally, research suggests that women in the fertile phase of their menstrual cycles discriminately inhibit sexually risky behaviors (Bröder & Hohmann, 2003), likely reducing the risk of sexual coercion.

Extant work on outgroup threat and conception risk provides less clear results. Early research findings demonstrated that women who were in the fertile phase of their menstrual cycles and who appraised themselves as vulnerable to sexual assault were less likely to accept date invitations from outgroup men (McDonald et al., 2011). However, other researchers have found that women are *more* attracted to outgroup men than ingroup men when near ovulation (Salvatore et al., 2017). It is possible that both findings hold true in different adaptive scenarios. Salvatore et al. (2017) suggests that fertile women are likely expressing attraction to outgroup men to increase genetic diversity of offspring in contexts where they feel safe and in control of mate choice, which differs greatly from contexts in which fertile women perceive sexual threat by outgroup men.

The costs of partner defection owing to perceived risk of infidelity and/or cuckoldry is expected to motivate a degree of rape fear that calibrates appropriate rape avoidance behavior among mated women. Thornhill and Thornhill (1990) found evidence of greater psychological distress following rape among married women, as opposed to single women. The greater psychological pain experienced by mated women is hypothesized to be an adaptive response that motivates avoidant behavior to reduce the likelihood of being raped again, given the greater risk of partner defection. Although research suggests that women in relationships perform a greater number of rape avoidance behaviors due to increased reproductive costs associated with partner abandonment (McKibbin et al., 2011; but see O'Donovan et al., 2007 and Snyder & Fessler, 2013b), in a more recent investigation of Thornhill and Thornhill's (1990) "relationship status hypothesis," Snyder and Fessler (2013a) found that women in cohabiting relationships are not more fearful of rape than single women. Instead, Snyder and Fessler (2013a) suggested that the male partners of rape victims may contribute to the psychological pain of relationship discord, owing to proprietary feelings toward their partner and/or discomfort surrounding being unable to protect their partner. In connection, an investigation of men's perceptions of sexually victimized women found that men perceive women who have been raped as less attractive, especially on the dimension of long-term mate attractiveness (Prokop & Pekárik, 2016). Moreover, mated men, to a greater degree than single men, rated raped women as less attractive. Although single women are 2.7 times more likely to be sexually victimized than married women (Wilson & Mesnick, 1997), it may be the case that single and married women experience similar FOR levels due to single women's lack of protection by male partners, mated women's desire to avoid partner defection, and similar desires among all women to cultivate positive sexual reputations to attract and/or maintain desirable mates (Perilloux et al., 2012). The mixed evidence likely suggests that both single and mated women engage in similar levels of rape avoidance behavior, owing to adaptive calibration of FOR.

Extending a Threat Management System for Rape Avoidance

There is sufficient evidence across scientific fields suggesting that women possess an evolved TMS for rape avoidance. We argue and provide evidence that perceptual cues signaling an increased risk of sexual victimization (e.g., age and dangerousness of environment) or that the reproductive costs of being targeted are heightened (e.g., via conception risk) serve as inputs to a TMS for rape avoidance. The combination of threat likelihood and reproductive costs

subsequently produce an adaptive emotional response, rape fear, which is calibrated accordingly to the magnitude of the perceived sexual threat. Motivated by that fear, a TMS for rape avoidance encourages adaptive behavioral outputs (e.g., defensive vigilance) that function to reduce sexual threat and protect women's reproductive choice. In support, recent research suggests that women who engage in more self-protective avoidance behaviors experience less subsequent sexual victimization (Gilmore et al., 2018).

The body of work that bolsters the argument for a TMS for rape avoidance does include limitations, however. Few, if any, studies have investigated the causal link between inputs that increase the likelihood of rape, FOR, and avoidance behaviors. Future research on individual factors that may increase the likelihood of being targeted for assault should focus on the associations between such factors and rape fear, with greater care toward controlling for age, as young women are disproportionately targeted for assault (Felson & Cundiff, 2014). Investigations of other characteristics among women from a TMS perspective, such as risk-recognition skills, may also provide insight on the ability to learn to perceive cues of sexual threat. Additionally, more work should be conducted to investigate the ambiguous relationship between kin proximity, FOR, and likelihood of victimization. Future studies investigating FOR should examine whether greater levels of fear correspond to greater engagement of behaviors that may reduce rape risk (e.g., stronger preference for formidable partners). Researchers should further investigate the various explanations for certain rape avoidance behaviors, such as whether heightened avoidance of outgroup men during ovulatory periods owes to greater FOR after accounting for perceptions of sexual threat. In sum, given the costs associated with sexual victimization (Romito & Grassi, 2007), it is important for future researchers to investigate other inputs, emotions, and behaviors that may be utilized in a TMS for rape avoidance, as well as to establish a causal link between the features of such a psychological system. However, as the burden of reducing sexual violence should not rest solely on the shoulders of women, future research should continue to investigate strategies to reduce sexual perpetration and other exploitative behaviors in men. Similarly, it possible that men evolved psychological adaptations to deter sexual victimization of their female kin, as doing so would likely protect their own reproductive fitness. Future work might investigate whether men possess psychological mechanisms that motivate them to protect female kin from sexual perpetrators when those women are at heightened risk of assault.

Note

1. Sexual coercion, sexual assault, and rape are operationally distinct phenomena. However, in this chapter, we discuss the full range of nonconsensual sexual acts that are typically distinguished by such terms with the terms “sexual assault,” “sexual aggression,” and “sexual violence.” Although vaginal rape incurs the most reproductive costs to women, because victims of sexual aggression cannot discern whether a sexual threat will result in rape, psychologically, it may motivate similar levels of psychological threat.

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PART VI

Mating and Endocrinology

CHAPTER
29

Hormones and Human Mating

James R. Roney

Abstract

Hormones are integral to the regulation of mating behavior in most sexually reproducing species and are likely to have similar importance for human mating. This chapter reviews major research themes regarding the role of endocrine variables in the adaptations that implement human mating psychology and behavior, including the roles of hormones in the development of sexual orientation, the regulation of sexual motivation and its trade-offs with competing motivational priorities, the relationship between hormones and attractiveness, and the role of hormones in the regulation of mate preferences. Investigation of the endocrine predictors of specific variables can help to arbitrate between competing theoretical arguments regarding human mating, and the chapter systematically reviews the relevant data on hormone variables within the context of these theoretical debates. As a broad generalization, accumulating evidence in humans supports roles for gonadal hormones in regulating shifts in the allocation of behavioral and somatic effort toward mating versus alternative adaptive problems. In women, evidence supports the ovarian hormones estradiol and progesterone acting as a two-signal endocrine code that indexes temporal fluctuations in fecundity and increases the prioritization of sexual motivation when fecundity is elevated. In men, accumulating evidence supports testosterone as a signal that regulates trade-offs between effort invested in mate-seeking and mate competition versus in survival effort and investment in pair- bonds and paternal care. Similar patterns in many nonhuman species suggest that phylogenetically ancient roles for hormones have been partially conserved in humans and continue to exert important effects on human mating psychology and behavior.

Key Words: estradiol, progesterone, testosterone, sexuality, menstrual cycle

Introduction: The Theoretical Framework Approach to Behavioral Endocrinology

Endocrine variables play major roles in the regulation of mating behaviors across sexually reproducing species. Hormonal signals both regulate and respond to gamete (i.e., sperm and egg) production and maturation, which makes these signals well-positioned to coordinate sexual psychology and behavior with the physiological conditions necessary for reproduction (Adkins-Regan, 2005). These statements are as true for humans as for other sexually reproducing species. This chapter reviews broad themes in the extant literature regarding the endocrine regulation of human mating psychology and behavior. The chapter takes a functional approach throughout in which hormones are viewed as signals that evolved to coordinate multiple, adaptive responses to the input conditions that trigger changes in hormone concentrations. I introduce that approach in what follows, before turning specifically to empirical research programs that investigate the endocrinology of human mating.

Theoretical Frameworks for Behavioral Endocrinology

Elsewhere, I have recently argued for a specific approach to building theories regarding the functions of hormones (Roney, 2016a). This approach is predicated on the well-supported observation that hormones are typically released into the general circulation, whereby they can affect multiple, diverse outcomes simultaneously. In many cases, these diverse outcomes can be seen as coordinated, adaptive responses to the input conditions that triggered changes in hormones. Given these premises, a logical way to build functional theories of endocrine signals is to catalog how input conditions that affect hormone production are mapped into coordinated output responses caused by the changes in hormones. I have called these listings of input–output mappings “theoretical frameworks” for specific hormones. The explicit construction of theoretical frameworks provides an efficient means of discovering the functions of endocrine signals (Roney, 2016a; see also Gangestad & Grebe, 2017).

A concrete example of a partial theoretical framework concerns seasonal shifts in male testosterone production in seasonally breeding species. During the breeding season, males of many species increase their testosterone production in

response to input cues such as photoperiod or the presence of fertile females; conversely, during the nonbreeding season, testosterone often falls to castrate levels (for reviews, see Daly & Wilson, 1983; Ketterson & Nolan, 1992; Muller, 2017; Wingfield et al., 1990). On the output side of the equation, androgens are well known to promote the growth of ornaments and armaments such as antlers, horns, or bright coloration; to support investment in skeletal muscle mass; but also to produce psychological and behavioral changes such as increased sexual motivation and intrasexual aggressiveness. Androgens appear to obtain energy for these output effects by suppressing energetic investments in survival-related functions such as immune responses and fat storage, and as a result, illness and food shortage are additional input conditions that reduce testosterone production in order to avoid these output effects when they would be especially harmful to survival prospects (see Bribiescas, 2001; Folstad & Karter, 1992; Ketterson & Nolan, 1992). Figure 29.1 summarizes this list of input conditions and output responses associated with seasonal changes in testosterone production in a way that provides a simple visual depiction of a partial theoretical framework.

Importantly, the theoretical framework depicted in figure 29.1 strongly suggests a core functional logic that *explains* the input–output mappings associated with testosterone rather than merely describing them. The output effects of elevated testosterone are multiple and diverse but are unified in promoting successful mate competition at precisely the time when such competition can facilitate reproductive success (i.e., when females are fecund during the breeding season). During the nonbreeding season when conception opportunities are absent, conversely, the drop in testosterone reduces the display of risky behaviors and reallocates energy into survival functions such as fat storage and immune responses, all of which should promote survival to the next breeding season in better physical condition. Natural selection may have used testosterone as the signal that mediates these input–output relationships because of its phylogenetically conserved role in the regulation of sperm production, since reproductively relevant inputs and outputs that were added over evolutionary time would all be efficiently coordinated with male fertility.

The theoretical framework approach becomes more complex when one considers that different aspects of input contexts can affect multiple hormonal signals simultaneously, all of which may interact to influence specific patterns of output responses. As explained more fully in Roney (2016a), the simultaneous influence of multiple endocrine signals can greatly expand the specificity and nuance of responses to specific variations in input conditions. Indeed, one can conceive of different combinations of baseline and reactive hormone values as endocrine codes that respond to adaptively relevant constellations of eliciting

conditions, and that in turn prime coordinated downstream effects that are functional responses to those circumstances. Looked at in this way, behavioral endocrinology is an exercise in code-breaking. The codes being cracked, furthermore, describe the functional properties of psychological adaptations that map adaptively significant input circumstances to the evolved responses to the inputs in question.

Theoretical Frameworks Related to the Endocrinology of Human Mating

The theoretical framework approach can also provide an integrated, functional perspective on the role of hormones in human mating psychology and behavior. At times in the extant literature, hormones are treated as somewhat arbitrary variables that are associated with certain mating-relevant outcomes, or as signaling devices that indicate attractiveness or other externally observable properties. Viewing hormones as internal signals that jointly mediate functional input–output mappings can help to explain why hormone concentrations might in some cases predict outcomes such as perceived physical attractiveness, while also potentially explaining circumstances under which such correlations will be absent.

The partial theoretical framework depicted in figure 29.1 provides a prototypical example of the way that hormones affect mating psychology and behavior. Hormones often act as signals that coordinate shifts in the investment of resources in mating effort versus in efforts to address alternative adaptive problems. This general principle can organize many findings regarding the roles of hormones in human mating psychology at a range of different timescales, as explained in the sections that follow. Much of this chapter focuses on activational (i.e., reversible, relatively short term) effects of hormones, but organizational (i.e., relatively irreversible, developmental) effects are also important for understanding human mating psychology and are reviewed first in the next section.

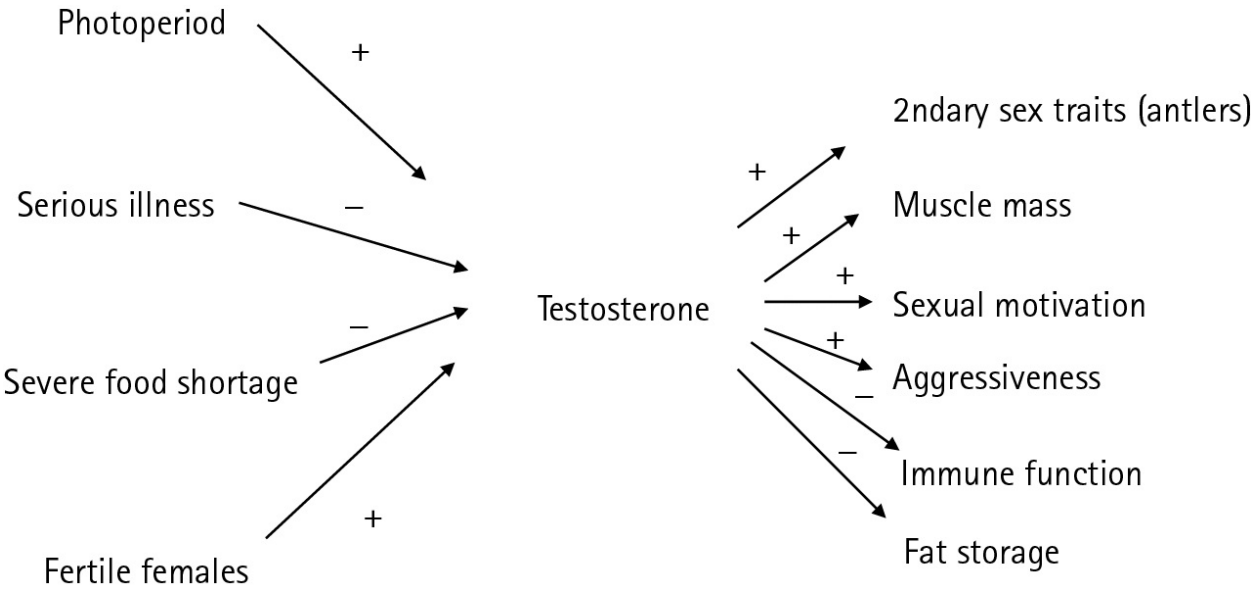

Fig. 29.1 An example theoretical framework depicting common input–output relationships for testosterone among males of seasonally breeding species.

Organizational Influences of Hormones on Human Mating Psychology and Behavior

It is well established that hormones exert organizational effects on the sexual differentiation of vertebrate phenotypes, including brain mechanisms that regulate mating behaviors. In mammals, genes on the Y chromosome promote prenatal development of testes that in turn lead to greater androgen production in males than in females; androgens like testosterone, in turn, alter gene expression governing development, providing a mechanism for the emergence of phenotypic sex differences (reviewed in Breedlove & Hampson, 2002). Organizational effects of hormones provide clear examples of the coordinating functions of endocrine signals, as they provide a broad means of coordinating sex-specific morphologies (including genitalia, reproductive tracts, and other sex-differentiated components of the body) with sexually selected behavioral strategies implemented by the brain. Given these organizational effects, it is likely that many sexually differentiated aspects of mating behaviors are influenced by hormones, making endocrine signals indispensable to comprehensive accounts of mating psychology and behavior.

In principle, variation in early hormone exposure may also explain within-sex variability in mating psychology and behavior. One prominent topic to which this idea has been applied is sexual orientation. In many nonhuman species, experimental manipulations of pre- or early postnatal androgen exposure can

produce sex-atypical sexual behaviors and partner preferences (e.g., Phoenix et al., 1959; reviewed in Adkins-Regan, 1988). In humans, more indirect evidence supports early androgen exposure as a cause of sexual orientation. First, individuals with an XY karyotype who do not respond to androgens due to complete androgen insensitivity syndrome (CAIS) present a female-typical external phenotype and report sexual attraction to men (e.g., Wisniewski et al., 2000; reviewed in Motta-Mena & Puts, 2017). This supports the necessity of androgen signaling for male-typical development and gynephilia (i.e., attraction to women) in humans. Second, the possible attribution of androphilia (i.e., attraction to men) in CAIS individuals to socialization as females and not to androgen deprivation is refuted by cases in which XY individuals with male-typical prenatal androgen exposure were reared as females. These cases involved either surgical accidents that damaged the penis in infancy or cloacal exstrophy (an abdominal abnormality that causes malformation of the penis), and entailed both early surgical reassignment and social rearing as females. Despite these interventions, in all seven cases in which published studies surveyed sexual attraction after puberty, the individuals in question reported predominant or exclusive attraction to women (reviewed in Bailey et al., 2016). Third, XX karyotype individuals with congenital adrenal hyperplasia (CAH)—a condition in which prenatal androgens can be highly elevated—often experience partial masculinization of genitalia and higher rates of gynephilia than do women without CAH, although the majority of such women do in fact report predominant attraction to men (Bailey et al., 2016). Thus, all of these cases demonstrate associations between prenatal androgen exposure and human sexual orientation, and indeed these and other lines of evidence support a dose-related relationship between amount of prenatal androgen exposure and the likelihood of exhibiting androphilia versus gynephilia (Motta-Mena & Puts, 2017).

Although the above lines of evidence strongly support a role for prenatal androgens in the determination of human sexual orientation, it is nonetheless the case that hormone exposure alone does not appear fully explanatory. For instance, women with CAH in some cases have prenatal androgen exposure comparable to males and yet the majority of such women report sexual attraction to men. This and other evidence led Bailey et al. (2016) to suggest that something other than androgen exposure that is associated with the Y chromosome may predict gynephilia, although whatever that might be cannot be completely necessary or there would be no cases of XX karyotype individuals experiencing attraction to women.

Rice et al. (2012) presented a theory of epigenetic influences on human sexual orientation that can potentially resolve ambiguities associated with

hormonal influences. They reviewed evidence that in both rats and humans, the degree of prenatal androgen exposure shows more overlap between the sexes than is commonly appreciated. This in turn should exert selection pressures to canalize degree of androgen signaling to avoid discordances between genital and brain development. Epi-marks (such as DNA methylation) that are added during early embryogenesis are capable of amplifying or blunting androgen signaling. Rice et al. proposed that such epi-marks are the canalizing mechanism that prevents fluctuations in prenatal androgen exposure from producing development that is discordant with genital sex. Homosexuality then results when an epi-mark inherited on a gamete from an opposite-sex parent fails to be erased during early development and is stronger in its effects than the new epi-mark that is added during embryogenesis. They also presented a mathematical model of selection pressures demonstrating that mutations for such canalizing epi-marks can invade a population under a range of plausible parameter values when the fitness costs of same-sex attraction are limited by such attraction being expressed in only a relatively small percentage of opposite-sex offspring. Eventually, over time, modifier loci that limit carryover of parental epi-marks that affect androgen signaling related to sexual attraction would be expected to evolve, but time lags may be common for this variable given that the stimuli that determine sexual attraction change frequently with speciation events.

The theory presented by Rice et al. (2012) has not been definitively tested via identification of the relevant epi-marks, to my knowledge, but its logic can account for many known patterns. Relatively low rates of gynephilia in XX karyotype women with CAH make sense, for instance, if such women have female-typical epi-marks that blunt the effects of their elevated prenatal androgens. Likewise, since epi-mark erasure and addition are somewhat stochastic during development, the theory can account for discordances between monozygotic twins in sexual orientation (reviewed in Bailey et al., 2016). Importantly, epi-marks can be specific to different targets of androgen signaling, which can help account for the mosaic nature of same-sex sexual orientations in that, for example, somatic development is usually sex typical even as the target of sexual attraction is sex atypical. Finally, the theory is consistent with all of the positive evidence for the organizing effects of hormones on sexual orientation, while resolving some empirical anomalies associated with the prenatal hormone hypothesis.

Epigenetic influences add considerable complexity to the study of organizational effects of hormones in humans since variables like epi-marks are very difficult to measure and can vary in their influences across different outcomes. Nonetheless, research has attempted to examine putative markers of

early androgen exposure in order to explain within-sex variability in additional mating-relevant variables other than sexual orientation. For example, the ratio of the lengths of the second to fourth digits on human hands (2d4d ratio) has been argued to reflect levels of prenatal androgen exposure during digit development (reviewed in Manning, 2002). Because androgens often organize the development of sexually selected traits in mammals, higher prenatal androgens indexed by 2d4d ratio could in principle explain trait-like, within-sex individual differences that persist into adulthood. Some research consistent with this has shown correlations between digit ratio and putatively androgen-dependent outcomes such as athletic ability, performance on spatial cognition tests, sperm production in men, levels of facial masculinity, and more dominant or aggressive behaviors (reviewed in Manning, 2002). However, some comparably powered attempts to test correlations between 2d4d and a suite of potentially androgen-dependent variables (including number of sex partners) have produced largely null results (e.g., Putz et al., 2004), and meta-analyses have reported either null or very small magnitude overall correlations between digit ratios and androgen-related behavioral variables (e.g., Hönekopp & Watson, 2011; Turanovic et al., 2017; Voracek et al., 2010; cf. Hönekopp & Schuster, 2010, for evidence of a reliable meta-analytic effect for measures of athletic ability).

Polymorphisms in the androgen receptor (AR) gene have also been investigated as possible influences on the organizational effects of hormones that may impact mating psychology and behavior. The number of cytosine-adenine-guanine (CAG) repeats in the AR gene varies continuously in humans, and evidence supports shorter repeat lengths predicting greater gene transcriptional activity mediated by the AR when the AR is bound by hormones like testosterone (Chamberlain et al., 1994). Because androgens regulate the expression of many different genes, polymorphisms in the AR gene could act as a type of dial that calibrates the magnitude of responses to circulating androgens in a coordinated way across the entire organism (see Simmons & Roney, 2011). This calibration should apply to both organizational and activational effects of hormones, with the expectation that individuals with shorter CAG repeat lengths will have more androgenized phenotypes per unit of androgen that they produce. Some studies have reported that men with shorter CAG repeat lengths exhibit stronger androgen-related outcomes related to intrasexual competition, such as greater muscle mass (Nielsen, 2010), physical strength (Simmons & Roney, 2011), and violent and aggressive behavior (e.g., Butovskaya et al., 2015; Rajender et al., 2008), although findings for these variables have been mixed and appear to vary across different ecological environments (Campbell et al., 2009; Ryan et al., 2017). Because androgen-dependent outcomes jointly depend on

both androgen production and AR sensitivity, polymorphisms in the AR gene alone may not consistently predict phenotypic outcomes due to both developmental and contextual variability in hormone production. Rather than strongly predicting trait-like individual differences in mating-relevant traits, then, AR gene polymorphisms may have more explanatory power as moderators of the effects of context-specific shifts in hormone production (e.g., Roney et al., 2010).

In summary, converging lines of evidence support an important role for prenatal hormones in causing the development of human sexual orientation, and there is every reason to believe that similar organizational effects of hormones cause the sexual differentiation of brain mechanisms involved in other aspects of human mating psychology. The study of organizational effects of hormones in humans is especially challenging, however, given the inability to experimentally manipulate early hormone exposure. Attempts to use measurable markers of the magnitude of early hormone exposure have met with mixed success in predicting phenotypic outcomes in adulthood, perhaps in part because there are many complex modifiers of androgen signaling, some of which, like epi-marks, are difficult to measure. Furthermore, if hormones do have as a basic function the coordination of adaptive responses to input circumstances that change over time, then we might expect a priori that activational effects of hormones that respond to such circumstances will not be overly constrained by quantitative differences in within-sex early hormone exposure. The functional logic of such activational effects of hormones is the focus of the rest of this chapter.

Ovarian Hormones and Human Mating

An interesting aspect of the theoretical framework approach is the possibility that multiple hormones can combine in their effects to jointly coordinate functional responses to the eliciting conditions that triggered the changes in hormone concentrations. Here, I argue for a simple, two-signal endocrine code involving ovarian hormones that follows a straightforward functional logic. This two-signal system appears to be expressed in some form in most mammalian females that have been investigated, and I review evidence that it is also conserved in humans. The argument here surely entails simplifications of the relevant physiological processes, but it is also heuristically useful in providing a functional framework for organizing research findings on ovarian hormones.

Estradiol and Progesterone as a Two-Signal Endocrine Code

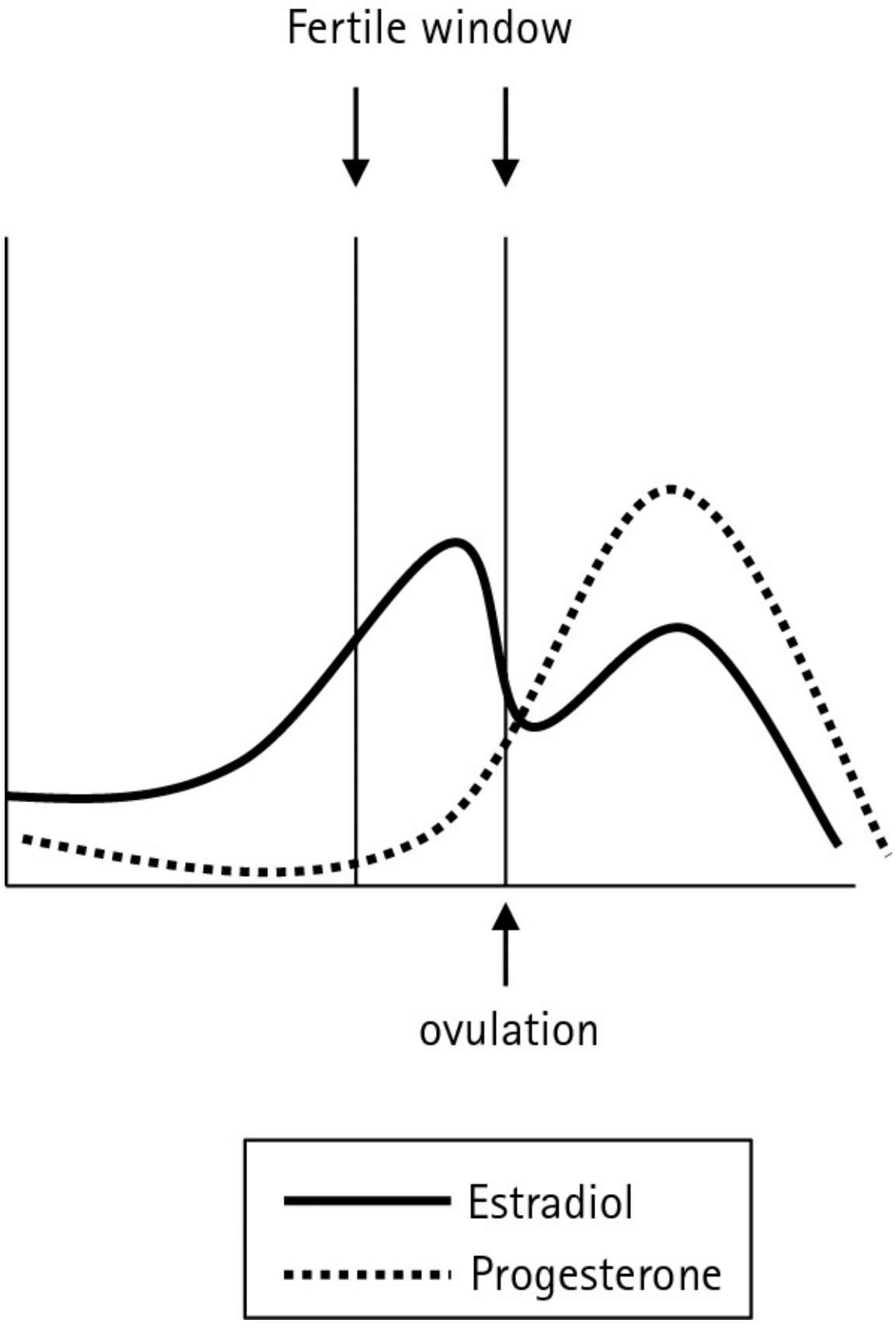
Fertile window
ovulation
Estradiol
Progesterone

Fig. 29.2 Prototypical patterns of estradiol and progesterone secretion in ovulatory human menstrual cycles. From left to right, the "follicular phase" runs from the first day of menstruation until the day of ovulation; the "luteal phase" is all days after ovulation. The fertile window represents days when conception is possible.

Figure 29.2 depicts the prototypical patterns of estradiol and progesterone production in an ovulatory human menstrual cycle. The increase in estradiol that occurs in the approach to ovulation is produced by the dominant follicle (the ovum and its surrounding support cells, with the latter producing estradiol) and is itself part of the mechanism that triggers the luteinizing hormone (LH) surge that causes ovulation, such that, as in other species, the estradiol surge is a reliable signal of impending ovulation. After ovulation, the follicle becomes a new structure called the corpus luteum, which continues to secrete estradiol but also secretes progesterone in high concentrations. The fertile window denotes the days of the cycle in which conception is possible, which in humans runs from approximately five days before ovulation through the day of ovulation itself (Wilcox et al., 1998). Estradiol and progesterone have local functions in the reproductive tract where they prepare the endometrium for possible attachment of a zygote and development of a subsequent embryo and fetus (reviewed in Hall, 2019; Lessey & Young, 2019), but they are also released into the general circulation whereby they can reach brain mechanisms that regulate psychology and behavior.

My proposal is that brain mechanisms largely read changing estradiol and progesterone concentrations as signals of *fecundity* (i.e., the likelihood of successful conception and subsequent gestation given unprotected copulation) (see Roney, 2015). It can be seen from figure 29.2 that the combination of high estradiol and low progesterone can be read as a code denoting high fecundity, whereas high progesterone itself can indicate low fecundity (at least at the within-cycle timescale). Thus, a simple way to increase the expression of a given behavior during high fecundity is to have brain mechanisms that promote the behavior be primed by estradiol but inhibited by progesterone, which should tend to couple the behavior to the fertile window. Conversely, specific behaviors can be reduced during the fertile window by reversing the direction of these effects, such that estradiol is inhibitory and progesterone excitatory. In this way, estradiol and progesterone can act as a simple two-signal endocrine code that coordinates behaviors with fecundity-relevant events in the reproductive tract.

There are clear functional reasons to increase the expression of sexual behaviors during fecund cycle days among females of most mammalian species. As an example, consider a rodent species in which males invest nothing in offspring other than genes. Females who engaged in sexual behavior when

conception was not possible in this species would risk predation, injury, or infection and also incur opportunity costs of invested time and energy in order to exhibit a behavior that had no current fitness benefits. When conception was possible, however, promoting its occurrence would bring large fitness benefits, especially since in a short-lifespan species with high mortality rates, missed conception opportunities in fecund cycles could have significant effects on rates of reproduction. Based on this simple functional analysis, one expects motivation to shift between sexuality and alternative priorities based on current fecundity.

Consistent with this expectation, in most mammalian females, sexual and feeding motivation exhibit opposite cycle phase shifts, with sexual receptivity either restricted to or greatly enhanced on days when conception is possible (reviewed in Adkins-Regan, 2005; Beach, 1976; Roney, 2015), but with feeding and foraging at their nadirs within the same species-specific fertile windows (reviewed in Fessler, 2003; Schneider et al., 2013). Estradiol and progesterone cause these shifts via the exertion of opposite effects on the two motivational priorities. Estradiol increases female sexual motivation in basically all nonhuman mammalian species that have been directly investigated (reviewed in Blaustein, 2008; Roney, 2015; Thornhill & Gangestad, 2008), whereas progesterone at luteal phase concentrations is inhibitory (reviewed in Roney et al., 2021). Conversely, estradiol administration reduces food intake in ovariectomized females, whereas subsequent progesterone injections in the same animals reverse the effects of estradiol and return eating to the ovariectomized baseline levels (e.g., Bielert & Busse, 1983; Kemnitz et al., 1989; reviewed in Asarian & Geary, 2006). This overall pattern of findings suggests that multiple brain mechanisms read estradiol and progesterone fluctuations as a two-signal code for fecundity, but by responding to this code in opposite ways, an increase in sexual motivation is coordinated with a decrease in feeding motivation during the fertile window when the relative fitness benefits of sexual behavior are at their highest.[1]

Is this two-signal endocrine code conserved in humans? Many studies have provided evidence that measures of women's sexual motivation are higher during the fertile window than at other times of the menstrual cycle (reviewed in Motta-Mena & Puts, 2017; Roney, 2015; Wallen, 2001). This pattern is consistent with effects of estradiol and progesterone given their secretion patterns across the cycle, but until recently, no studies had provided direct evidence for hormonal regulation of these shifts. In a daily diary study in which women were sampled across one to two menstrual cycles, my lab reported positive, within-cycle correlations between fluctuations in estradiol and self-

reports of sexual desire, and even larger negative correlations between progesterone and desire (Roney & Simmons, 2013). Jones et al. (2018a) also found negative within-women correlations between progesterone and self-reported desire in a sample of more than three hundred women sampled weekly for at least five weeks, as well some evidence for positive associations between estradiol and desire. More recently, Righetti et al. (2020) reported null within-cycle correlations between general sexual desire and changes in either estradiol or progesterone, although hormones were measured from urine samples that reflect broader and more variable temporal windows of hormone production than do the salivary measures that were collected in the prior studies. Thus, although further research on this question is warranted in humans, evidence supports estradiol and progesterone as opposing signals that regulate sexual motivation and that may causally generate fertile window shifts in women's sexual desire.

As in nonhuman mammals, evidence supports estradiol and progesterone having associations with women's feeding motivation that are opposite in sign to the hormones' associations with sexual desire. First, many studies have reported evidence for drops in women's food intake near ovulation when estradiol is high and progesterone low (Asarian & Geary, 2006; Fessler, 2003). Second, women in the Roney and Simmons (2013) study in which we assessed hormonal predictors of sexual desire were also surveyed about their daily food intake. For this dependent variable, we found that within-cycle changes in estradiol negatively predicted day-to-day changes in amount eaten, progesterone fluctuations positively predicted them, and the two hormones together statistically mediated a drop in food intake during the fertile window (Roney & Simmons, 2017). These findings support a phylogenetically conserved role for ovarian hormones in shifting women's motivational priorities between sexuality and alternative adaptive problems based on whether conception is currently possible.

The idea that an important function of hormones is to regulate shifts in the prioritization of alternative adaptive problems is a position that I have labeled "motivational priorities theory" (Roney, 2018).[2] Motivational priorities theory can be extended beyond the timescale of individual menstrual cycles in addressing the functions of ovarian hormones. For example, shifts in sexual motivation associated with lactation (during which sexual desire generally declines), menopause, and hormone replacement therapy all provide further evidence for this position in humans (reviewed in Roney, 2015, 2016a, 2018). Ovarian hormones have phylogenetically ancient roles in calibrating mating motivation, and such effects are likely to be foundational for understanding endocrine influences on mating dynamics in humans. Nonetheless, human

mating systems have some relatively unique properties that may have changed the roles of ovarian hormones relative to other mammalian species. Some of those properties are addressed in the next section.

Extended Sexuality, Pair-Bonding, and Endocrine Predictors of Female Attractiveness

Contrary to most mammals in which sexual behavior is often largely confined to the fertile window, humans engage in high rates of nonconceptive sex, referred to as "extended sexuality." Extended sexuality is argued to evolve when females obtain material, nongenetic fitness benefits from nonconceptive sex (see Thornhill & Gangestad, 2008). In humans, those benefits were likely related to pair-bonding and its associated male investments in the welfare of their mates and offspring. Most major theories of the evolution of human pair-bonding posit that concealed ovulatory timing was a necessary step for the emergence of male investments in long-term mating (e.g., Lovejoy, 2009; Strassmann, 1981; Symons, 1979). Since sexual behavior confined to the fertile window would reliably reveal ovulatory timing, these arguments posit an extension of sexual receptivity beyond conceptive cycle days as part of the evolution of human pair-bonding. Based on these ideas, the basic biological function of women's extended sexuality is the formation and maintenance of long-term pair-bonds.

Elsewhere, I have argued that nonhormonal, social inputs to brain mechanisms regulating women's sexuality have effects that are additive to hormonal influences and that largely explain human extended sexuality (Roney, 2018). For example, research supports new relationship status as a positive predictor of women's sexual desire, and dyadic variables such as relative commitment to the relationship across the two partners may also moderate women's desire and rates of sexual initiation (reviewed in Roney, 2018, 2019). Such social inputs are proposed to promote the initiation and maintenance of pair-bonds, and by responding to social variables in a hormone-independent way, can maintain sexual receptivity even during anovulatory time periods. Thus, women's sexual motivation is proposed to be regulated by two broad input pathways: (1) a hormone input pathway that shifts motivation toward sexuality during the fertile window when the net ancestral fitness benefits of sex were likely to have been elevated, on average, and (2) a social input pathway that responds to mating opportunities and relationship dynamics to promote successful romantic relationships. Consideration of how these two pathways combine in their effects can be used to explain contexts in which women's sexual desire is elevated and conversely to explain cases of hypoactive sexual

desire (Roney, 2019). The two-input pathway position is also important for understanding the limits of endocrine influences on women's sexuality, since in many contexts social variables may have stronger effects than do hormonal inputs.[3]

These arguments for the evolution of pair-bonding and extended sexuality carry implications for the possible effects of ovarian hormones on women's attractiveness. In many nonhuman species for which sexuality is largely confined to fecund cycle days, females often emit diagnostic cues of ovulatory timing, such as genital swellings or changes in odor (reviewed in Coombes et al., 2018; Dixson, 1998). Furthermore, as one would expect from the hormone secretion patterns depicted in figure 29.2, the same two-signal endocrine code implements these effects, with evidence supporting positive effects of estradiol and negative effects of progesterone on cues such as odor attractiveness across a range of different mammalian species (e.g., Baum et al., 1977; Ferkin & Johnston, 1993; Lucas et al., 1982; Michael et al., 1976). Concealment of ovulatory timing is a major component of theories for the evolution of human pair-bonding, however, which raises questions regarding the conservation of such hormone effects in humans.

Studies have reported that women's voices, odors, and faces are rated more attractive, on average, during the fertile window than at other times of the menstrual cycle (reviewed in Haselton & Gildersleeve, 2011, 2016). Some authors have suggested from such findings that human ovulation is not actually concealed (e.g., Kuukasjärvi et al., 2004; Singh & Bronstad, 2001). There is a clear tension between such statements and theories about the evolution of human pair-bonding. Data regarding the endocrine predictors of cycle phase shifts in stimulus attractiveness can contribute to this debate.

First, a statistically significant change in stimulus attractiveness does not necessarily mean that a cycle phase shift is large enough to be diagnostic of ovulatory timing. As an example of this, Havlíček et al. (2006) showed that although women's odors were on average rated more attractive when collected at midcycle than when collected during menstruation or in the estimated luteal phase, it was nonetheless the case that between-women variability in odor attractiveness was much greater than within-cycle variability. This means that some women smelled consistently better outside the fertile window than did other women inside, which essentially leaves odor perceivers without clearly diagnostic information regarding ovulatory timing (see Roney, 2009). This is relevant to hormone effects, as well, since research designs may be able to detect statistically significant hormonal predictors of stimulus attractiveness that are nonetheless too subtle to be diagnostic of fertile window timing.

Second, different hormonal predictors of stimulus attractiveness carry different implications regarding the detectability of ovulatory timing. A positive effect of estradiol alone, for example, would not necessarily provide much information regarding ovulatory timing given between-women and between-cycle variability in production of this hormone. Estradiol tends to be elevated in cycles with greater conception probability (Lipson & Ellison, 1996). Figure 29.3 depicts estradiol production across two different ovulatory cycles, which could represent cycles from different women or from the same woman at different times. It can be seen from the figure that estradiol can be higher during the luteal phase of a higher fecundity cycle (point A) than it is inside the fertile window of a lower fecundity cycle (point B). Positive regulation of odor attractiveness by estradiol alone, then, would lead to cases in which nonfecund samples (point A) are rated more attractive than fertile window samples (point B), thus making odor an unreliable indicator of ovulatory timing (notice that even a woman's own partner could mistake point A as a fertile window day if their partner smells more attractive than usual on that day). Negative effects of progesterone on attractiveness, if large enough, by contrast, would more consistently reduce stimulus attractiveness during the luteal phase, after the fertile window had ended (see fig. 29.2).

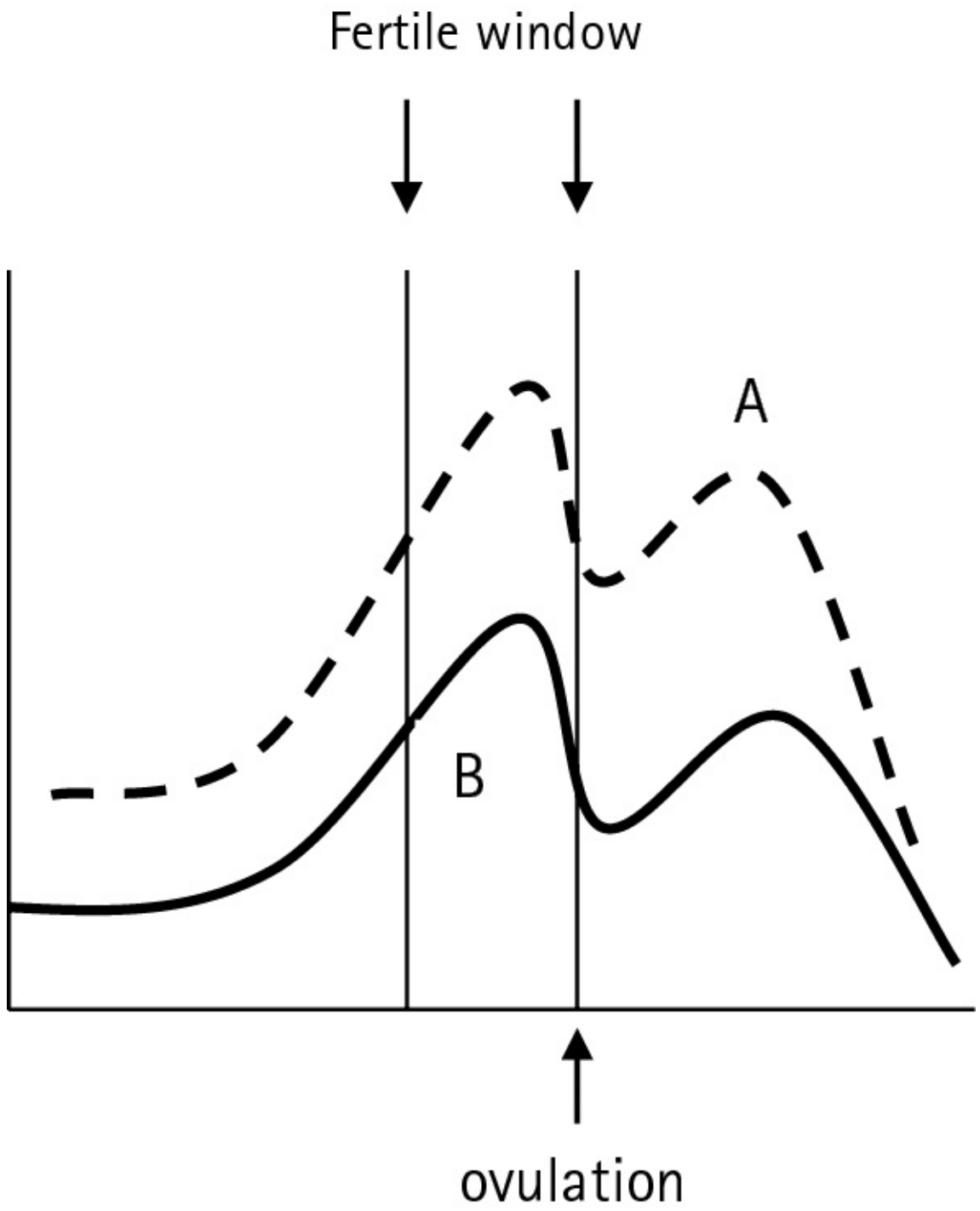

Fig. 29.3 A depiction of estradiol secretion across cycle days of two different menstrual cycles that differ in their overall estradiol production.

These considerations suggest that one evolutionary pathway for concealing ovulatory timing might involve suppression of effects of progesterone on perceivable stimuli. If estradiol continued to affect stimuli, however, selection

may have maintained men's preferences for cues associated with higher estradiol because those cues predicted higher fecundity between cycles or across different women. In that case, within-cycle shifts in stimulus attractiveness would be by-products of mechanisms that track overall concentrations of estradiol (see Havlíček et al., 2015; Roney, 2009). In sum, positive effects of estradiol combined with weakened effects of progesterone on women's stimuli could generate shifts in women's attractiveness that follow the same patterns as the estradiol curves depicted in figure 29.3. Those patterns can generate subtle within-cycle shifts in attractiveness that nonetheless leave ovulatory timing effectively concealed.

Does existing evidence support primary regulation of cycle phase shifts in attractiveness via positive effects of estradiol? Puts et al. (2013) did not find that change in estradiol across two cycle days predicted change in women's face or voice attractiveness. However, the two days compared—near ovulation and in the estimated midluteal phase—do not typically differ much in mean estradiol. Their study did find a negative correlation between change in progesterone and change in both types of attractiveness, although there was such large variability between women in whether their high or low progesterone days were rated more attractive that it is unlikely that perceivers could extract reliable information about ovulatory timing. Furthermore, Jones et al. (2018c) failed to replicate a negative within-women relationship between changes in progesterone and changes in face attractiveness when photos and hormones were sampled more evenly across the cycle at five weekly intervals (within-women associations between estradiol and face attractiveness were also null). Other research has shown that face morphs constructed from photos taken on cycle days when measured estradiol was higher were ranked more attractive than morphs of the same women created from photos taken was estradiol was lower (Catena et al., 2019; cf. Bobst & Lobmaier, 2012). More indirectly supporting hormone effects, Miller et al. (2007) showed that tips received by lap dancers were distributed across the cycle in a way that closely mimicked the prototypical estradiol curve (see their Miller et al., 2007, fig. 1), which is consistent with attractiveness changes tracking estradiol but not progesterone.

The above evidence is inconclusive regarding hormonal predictors of within-cycle shifts in the attractiveness of women's stimuli, and further research is necessary. Notably, no published studies have tested hormonal predictors of within-women shifts in odor attractiveness, despite the important role of odors in signaling ovulatory timing in many nonhuman species. A study similar to Jones et al. (2018c) but assessing hormonal correlates of odor attractiveness repeatedly across the full cycle would be especially valuable for adjudicating how

endocrine influences on cycle-associated stimuli may have changed in humans relative to many nonhuman mammals.

Other research has assessed between-women relationships between hormones and attractiveness. These studies assess whether, for instance, a woman represented by the top estradiol curve in figure 29.3 would tend to be rated more attractive than one represented by the bottom curve. Since conception cycles are associated with higher estradiol production (Lipson & Ellison, 1996), evidence for such a correlation would support the idea that human attractiveness judgments track fitness-relevant properties, such as conception probability. This in turn would corroborate other evidence (e.g., Gangestad & Scheyd, 2005) that argues against the idea that attractiveness judgments are arbitrary social constructions, since on the social construction account the hormone correlations would be unexplained coincidences.

Initial evidence for such hormone correlations was promising. In a study of more than one hundred women with daily hormone values across a full menstrual cycle, Jasienska et al. (2004) reported that women with lower waist-to-hip ratio (WHR) and larger breasts had higher estradiol and progesterone concentrations than did other women. Features like low WHR are rated attractive in women (e.g., Singh, 1993), though Jasienska et al. did not collect attractiveness ratings of the women in their sample. Law-Smith et al. (2006) reported that women with higher estradiol (measured from one or two urine samples in the estimated late follicular phase) had face photographs that were rated more attractive, though their estimation of cycle region was imprecise and their finding based on a small sample of women who were not wearing makeup (n = 30). Finally, Durante and Li (2009) averaged two estradiol values per woman (collected from near ovulation and in the luteal phase) in a sample of forty-five women, and found a positive correlation between women's mean estradiol concentrations and attractiveness ratings of their photos in which both bodies and faces were visible.

More recent studies have not consistently replicated between-women relationships between hormones and determinants of women's attractiveness. Grillot et al. (2014), in a study with daily hormone values, found no evidence that women with lower WHR or larger breasts had higher estradiol or progesterone, though the sample size (n = 33) was smaller than in Jasienska et al. (2004). The Grillot et al. study did report a positive partial correlation between ratings of women's body attractiveness and their mean estradiol concentrations when body mass index (BMI) was held constant, though replication of that unpredicted finding has not been assessed. In a large sample of nearly 250 women, Jones et al. (2018c) found that mean estradiol computed over five

weekly samples per woman was *positively* correlated with measurements of women's WHR, opposite to the finding from Jasienska et al. (2004). Furthermore, Jones et al. reported null associations between mean estradiol and progesterone and ratings of women's face attractiveness, thus failing to replicate findings that were reported by Law-Smith et al. (2006) with a much smaller sample size.

The overall evidence for between-women relationships between ovarian hormones and physical attractiveness is thus mixed and inconclusive. It is not entirely clear that consistent effects should be expected, however. Ovarian hormones fluctuate across time within-women based on energetic variables (reviewed in Ellison, 2001), which in turn can be seen as input conditions for the initiation of ovulatory cycles in theoretical frameworks for ovarian hormones (Roney, 2016a). Studies that have measured ovarian hormones have obtained snapshots of their production within a given cycle, but hormones can vary considerably across cycles within women even in well-nourished populations (see Lipson & Ellison, 1996), whereas variables like facial attractiveness or WHR may be much more stable over similar time-periods. This should add considerable noise to hormone-attractiveness correlations. Finally, within-women, between-cycle effects of hormones on women's attractiveness (e.g., in fig. 29.3, is the same woman more attractive when in a cycle characterized by the top vs. the bottom estradiol curve?) have never been tested. Although challenging, such tests—especially for more state-like traits like odor or voice attractiveness—could provide important evidence regarding whether men's preferences mechanisms are primarily tracking between- rather than within-cycle indicators of fecundity.

In summary, human pair-bonding may have altered some aspects of the two-signal endocrine code that can be used to understand ovarian hormones in many nonhuman species. Endocrine influences on sexuality have weakened relative to social influences in humans, facilitating an increase in extended sexuality that may have promoted investment by long-term pair-bond partners over the course of human evolution. Suppression of some hormone effects on women's observable stimuli may have been important for sufficient concealment of ovulatory timing to promote pair-bonding, although more detailed research on the hormonal predictors of within-cycle attractiveness shifts is necessary to test precisely how this may have occurred. Finally, existing evidence is insufficient to support the conclusion that more attractive women tend to have higher ovarian hormone production, although such effects might be detectable if it were possible to account for between-cycle variability in hormone production by measuring hormones over longer stretches of time.

Dual Sexuality, Hormones, and Women's Mate Preferences

The argument that estradiol and progesterone act as a two-signal endocrine code that calibrates motivational priorities to fluctuations in fecundity is well supported across many nonhuman species and, as reviewed above, is also supported by evidence in humans. Nonetheless, the human cycle phase literature has been dominated by an alternative theoretical perspective known as "dual sexuality theory." Prominent versions of this perspective have posited that women's sexual psychology is qualitatively different inside the fertile window than at other times of the cycle: attraction to and desire for men with markers of high genetic quality are elevated in the fertile window, but attraction to and desire for high investing pair-bond partners are elevated outside the fertile window, and especially in the luteal phase (reviewed in Thornhill & Gangestad, 2008). One functional explanation for this shift is that it implements a mixed-mating strategy in which ancestral women could obtain direct benefits from high investing pair-bond partners at most times but could obtain higher-quality genes from extra-pair men by committing infidelities with them during the fertile window when conception was possible (e.g., Gangestad et al., 2002; Penton-Voak et al., 1999).

A version of dual sexuality theory could be compatible with motivational priorities theory if it were the case that there is a general increase in sexual motivation during the fertile window but that women also exhibit stronger attraction to markers of good genes at that time. Proponents of dual sexuality theory have argued, however, that sexual motivation in general does not increase near ovulation (Gangestad et al., 2002; Haselton & Gangestad, 2006) (instead, only desire for men with markers of high genetic quality increases), that most women do not experience increased desire for their long-term partners in the fertile window (Gangestad et al., 2002; Pillsworth & Haselton, 2006), and that, if anything, desire for own partners is higher during the luteal phase when progesterone is elevated (Grebe et al., 2016). These conclusions—based on results from studies that generally collected only two data points per cycle—if true, would refute motivational priorities theory, which posits that sexual motivation in general trades off against alternative motivational priorities under the influence of fecundity-signaling ovarian hormones. However, daily diary studies with much larger numbers of sample days within-women have shown that all measures of sexual motivation, including desire for and sex with women's own long-term partners, tend to increase near ovulation and to decline during the luteal phase when progesterone is elevated (Arslan et al., 2021; Roney & Simmons, 2016; Shimoda et al., 2018; Wilcox et al., 2004). There is ongoing

debate about whether the size of cycle phase shifts in desire is moderated by the attractiveness of women's partners (e.g., Larson et al., 2012), but as a main effect, evidence is converging on the conclusion that in-pair desire and sexual activity increase during the fertile window, consistent with predictions from motivational priorities theory (reviewed in Roney, 2018).

Most research on dual sexuality has focused on mate preferences, however, rather than sexual desire. The "ovulatory shift hypothesis" predicts that preferences for putative markers of genetic quality—including facial and body masculinity, deeper voice pitch, and more dominant behaviors—increases during the fertile window specifically when women are rating stimuli for short-term, sexual attractiveness (Gildersleeve et al., 2014). Although many studies initially supported this hypothesis, a number of more recent investigations with precise determination of ovulatory timing have failed to replicate these findings (reviewed in Jones et al., 2019). Because there is a separate chapter on cycle phase effects, I will not specifically review these studies (see Stern & Penke, this volume). Rather, in what follows, I suggest how knowledge of the hormonal predictors of cycle phase shifts may inform this debate.

From inspection of figure 29.2, a straightforward proximate means of implementing the effects postulated by the ovulatory shift hypothesis would entail positive effects of estradiol combined with negative effects of progesterone on preferences for masculine features. The mixed-mating explanation for cycle phase shifts should predict very strong inhibitory effects of progesterone on preferences for masculine traits, since the genetic benefits of stealth infidelity are impossible to obtain during the nonfecund luteal phase, but the costs of being caught in an infidelity remain at that time. Thus, on the infidelity-based model, empirical studies should detect strong negative correlations between progesterone and attraction to putative fitness indicators.

Elsewhere, my collaborators and I have proposed an alternative to the infidelity-based model of cycle phase shifts that we called "between-cycle theory" (Lukaszewski & Roney, 2009; Roney, 2009; Roney & Simmons, 2008). This theory proposes that women upregulate attention to markers of genetic quality during broad time periods when fecundity is elevated, rather than doing so only during the fertile windows of ovulatory cycles. In figure 29.3, for instance, the theory proposes a mechanism to increase attraction to fitness indicators when moving from the lower to the higher fecundity cycle represented by the two estradiol curves. The lower curve could occur during events such as lactation when hormones and fecundity are suppressed, and when partner evaluation may be focused on crucially important direct benefit provisioning at that time. But with a return to more fecund cycles (represented by the higher

curve), the weighting placed on potential mates' genetic quality may increase at a time when partner switching could occur before the next conception. On this position, the mechanism in question is responding to overall cycle fecundity and not to fertile window timing, and thus there is no reason to expect inhibitory effects of progesterone on attraction to putative cues of genetic quality. Instead, between-cycle theory predicts that attraction to fitness indicators will correlate positively with estradiol concentrations. Between-cycle theory and the mixed-mating hypothesis thus generate similar predictions regarding effects of estradiol on women's preferences for cues of men's genetic quality, but mixed-mating theory uniquely predicts inhibitory effects of progesterone on such preferences.

What does the extant literature show regarding hormonal predictors of women's attraction to masculine features in men? Recent studies have consistently reported null associations between within-cycle shifts in measured progesterone concentrations and within-cycle shifts in women's preferences for masculine behaviors, voices, bodies, and faces (Ditzen et al., 2017; Jones et al., 2018b; Jones et al., 2018d; Jünger et al., 2018b; Marcinkowska et al., 2018; Pisanski et al., 2014; Stern et al., 2020). Gangestad et al. (2019) argued for a negative association between progesterone and attraction to measures of men's body masculinity in partnered women only in a reanalysis of data from Junger et al. (2018a), but their reanalysis was challenged by the original authors (Stern et al., 2019); furthermore, that same association in partnered women was not found in Marcinkowska et al. (2018). Thus, a striking finding from recent hormone studies of mate preferences—some of which, like Jones et al. (2018b), were very highly powered—is an overall lack of evidence for inhibitory effects of progesterone on preferences for putative good genes indicators in men. Because the infidelity-based mixed-mating hypothesis should predict strong inhibitory effects of progesterone, as explained above, these results provide direct evidence against the mixed-mating model.

Evidence for the between-cycle theory has been more mixed. Two initial studies reported that women's estradiol concentrations positively predicted their attraction to faces of men with higher measured testosterone concentrations (Roney et al., 2011; Roney & Simmons, 2008); combined with null results for progesterone, these findings were consistent with predictions from between-cycle theory. In Roney et al. (2011), however, this effect was not found for women's ratings of artificially masculinized faces, suggesting a possible dissociation between preferences for cues of testosterone and preferences for some measures of facial masculinity. Jones et al. (2018b), in the highest-powered investigation of women's preferences for facial masculinity yet conducted (at least five weekly measurements in more than three hundred women), also

reported null within-women associations between changes in estradiol and changes in attraction to artificially masculinized faces. Some evidence for positive associations between estradiol and preferences for face masculinity was reported in Ditzen et al. (2017), albeit in a smaller sample than in Jones et al. A series of studies by Junger and colleagues reported null within-women associations between estradiol and preferences for various masculine traits (Jünger et al., 2018a; Jünger et al., 2018b; Stern et al., 2020), but these studies all compared the late fertile window to the midluteal phase, which are time periods across which estradiol does not vary much. Finally, Pisanski et al. (2014) reported marginally significant within-women correlations between estradiol and preferences for deeper voice pitch in men among a sample of sixty-two women tested across five weekly sessions; when this sample was expanded to more than three hundred women, however, a robust positive effect of estradiol on attraction to deeper voices was found (Jones et al., 2018d). Thus, although findings are mixed and further research appears necessary, evidence supports stronger attraction to facial cues of high testosterone and to lower voice pitch when women's estradiol is elevated. These positive findings—in conjunction with null effects for progesterone in the same studies—provide some evidence consistent with between-cycle theory.

In summary, a series of recent studies have provided new evidence regarding hormonal predictors of women's mate preferences. These studies are generally consistent in finding null effects of progesterone on preferences for masculine traits in men, which argues against the mixed-mating hypothesis. Some but not all findings have supported positive correlations between estradiol and preferences for masculine traits. Although within-cycle correlations between estradiol and preferences for putative fitness indicators are consistent with predictions from between-cycle theory, a more direct test of the theory would entail comparing the same women's preferences across cycles with higher versus lower production of estradiol (as in fig. 29.3). It is possible, however, that the few positive findings for effects of estradiol on women's mate preferences are actually false positives. In that case, rather than regulating mate preferences, ovarian hormones may primarily regulate shifts in women's sexual motivation, which is a phylogenetically conserved role for estradiol and progesterone across females of most mammalian species.

Testosterone and Human Mating

The partial theoretical framework presented for males of seasonally breeding species in figure 29.1 summarizes broad input–output patterns associated with

testosterone across many vertebrate species. These input–output relationships support an abstract characterization of testosterone as regulating trade-offs between investment in mating competition and investment in alternative adaptive problems. Functionally, because different adaptive problems vary in immediate importance across different contexts and time periods, having signals that can coordinate shifts in investments across the whole organism facilitates adaptive allocations of effort to those problems that are currently most pressing. Testosterone can be understood as one such signal.

The "challenge hypothesis" is an influential model of how testosterone shifts across time periods and contexts (Wingfield et al., 1990). The model was originally developed for understanding hormone effects in seasonally breeding birds, including among those that form pair-bonds. It suggests some refinements to figure 29.1 in the sense that testosterone production is posited to vary across three broad levels: very low production during the nonbreeding season; intermediate production in response to seasonal cues that serves as a breeding season "baseline," which increases expression of plumage ornaments, upregulates spermatogenesis, and produces sexual motivation sufficient for sexual behavior; and a maximal "challenge"-induced level that responds to competition with other males for territory establishment and access to and mate guarding of fertile females. In addition to the types of physiological effects summarized in figure 29.1, testosterone also clearly regulates shifts in male birds' motivational priorities between mate competition and paternal effort: exogenous administration of testosterone to fathers (at a time when their natural testosterone has typically fallen from challenge-induced concentrations) increases their courtship and competitive behaviors at the cost of reduced paternal provisioning of offspring, leading to substantial increases in juvenile mortality (e.g., Hegner & Wingfield, 1987). The general pattern described by the challenge hypothesis can be used to organize findings about how testosterone production varies across time in human males and the role of such variability in regulating shifts in motivational priorities between mating effort and investment in alternative adaptive problems.

Testosterone and Men's Relationship Dynamics

Humans are not seasonal breeders, but they clearly move through life history stages that vary in degree of mate-seeking versus investment in alternative priorities, such as parenting. If effects of testosterone in allocating effort to mate competition are conserved in humans, then one would expect men's testosterone to be elevated when single and mate-seeking but to decline when pair-bonded

and investing in offspring. Relatively higher testosterone concentrations in single men may be loosely analogous to the intermediate, breeding season elevation of testosterone posited by the challenge hypothesis. If men's testosterone also responds to more immediate social events—interactions with potential mates or competitive challenges from same-sex rivals—then these further increases in testosterone could be seen as analogous to the challenge-induced maximal testosterone production posited by the challenge hypothesis. In what follows, I review evidence for both of these patterns in human males.

First, it is important to point out that the broader coordinating functions of testosterone seen in many nonhuman species do appear to be largely conserved in humans. Elsewhere, in developing a fuller theoretical framework for men's testosterone, I reviewed evidence that many of the inputs and outputs listed in figure 29.1 (minus the antlers, of course) also characterize human males (Roney, 2016a; see also Bribiescas, 2001). This helps make functional sense of a possible drop in men's testosterone when partnered or fathering, since some of the somatic effects of this hormone on outcomes such as immune function, elevated metabolic rate, and fat storage would have imposed ancestral survival costs that should have been avoided when diversion of energy was not needed for mate competition. Here, however, I focus more directly on psychological and behavioral variables related to mating, and the hypothesized role of testosterone in mediating shifts in motivational priorities.

A large number of cross-sectional (reviewed in Gray & Campbell, 2009; Roney & Gettler, 2015) and a few longitudinal (Gettler et al., 2011; Mazur & Michalek, 1998) studies have provided evidence for drops in men's testosterone after entry into committed romantic relationships, with even larger declines when partnering is coupled with the birth of children. In an important recent synthesis of this literature, Grebe et al. (2019) used meta-analysis to show that both relationship status and fatherhood are reliably associated with declines in men's testosterone when considering both published and unpublished studies. This pattern is consistent with the decline in testosterone associated with the hatching of offspring and onset of paternal effort in pair-bonding birds (Wingfield et al., 1990; for a review of similar patterns in nonhuman primates, see Muller, 2017), and represents an important endocrine signature of adaptive design for pair-bonding and paternal investment in humans.

Roney and Gettler (2015) characterized these temporal shifts in testosterone as a "testosterone-relationship cycle" in which a current focus on mate-seeking increases testosterone, testosterone promotes mating effort that increases the probability of entering a long-term relationship, but then relationship entry feeds back to reduce testosterone and further mating effort. Some longitudinal

evidence does support higher baseline testosterone increasing the probability of long-term relationship entry (Gettler et al., 2011), as well predicting dominance-related behaviors during mate competitions that enhanced perceptions of attractiveness (Slatcher et al., 2011). Furthermore, the importance of mate-seeking as a key variable is supported by evidence that men in relationships who maintain high sociosexual desire (i.e., interest in and arousal by extra-pair partners) maintain elevated testosterone despite being partnered (e.g., Edelstein et al., 2011; McIntyre et al., 2006). Edelstein et al. (2014) showed that men's testosterone concentrations were negatively associated with both their own and their partners' relationship satisfaction in a dyadic study of romantic couples, suggesting that increased testosterone was a cause or consequence of relationship dissatisfaction that may in turn be associated with seeking alternative mates. Indeed, other longitudinal research has reported that men's testosterone concentrations positively predict their future probability of divorce (Booth & Dabbs, 1993).

Research on men's testosterone has focused on its role in calibrating mate competition and status striving rather than predicting variability in men's sexual motivation. In many nonhuman species, only fairly low thresholds of testosterone production are necessary for full expressions of sexual behavior, and indeed the intermediate, breeding baseline level of testosterone production is sufficient for copulation in pair-bonding birds (Wingfield et al., 1990). A very similar pattern occurs in humans. Chemical suppression of natural testosterone production to very low concentrations does reduce men's desire, fantasy, and sexual behavior, but subsequent testosterone replacement at only half the average baseline concentration is sufficient to restore baseline measures of the sexual variables (Bagatell et al., 1994b). Conversely, supplementing men's natural testosterone production to concentrations much higher than their natural baselines did not increase their sexual desire or behavior (Bagatell et al., 1994a). Thus, testosterone fluctuations within the normal range appear to track men's mate-seeking motivation and mate competition efforts but do not strongly affect sexual desire itself, which instead requires only threshold concentrations of androgen production.

The endocrine regulation of men's sexuality thus appears substantially different than such regulation in women, for whom sexual desire is more continuously calibrated to fluctuations in estradiol and progesterone. Importantly, women's brain mechanisms have direct information regarding temporal fluctuations in fecundity via hormonal signals and can therefore adjust sexual motivation accordingly. If, however, women's ovulation is effectively concealed from other individuals, then an adaptive strategy for men may be to

desire sex at regular intervals with their long-term partners in order to capture concealed conception opportunities whenever they occur. Men's rates of sexual initiation appear to be flat across their partners' menstrual cycles (Adams et al., 1978; Caruso et al., 2014; VanGoozen et al., 1997; cf. Harvey, 1987), and some research has reported no changes in men's testosterone across distinct phases of their partners' cycles (Ström et al., 2012; Ström et al., 2018). These patterns are consistent with ovulatory timing being effectively concealed. Men's sexual motivation requiring only low-threshold concentrations of testosterone may facilitate this strategy of somewhat continuous sexual desire as a response to concealed ovulation. In addition, full sexual function in response to low thresholds of androgen production allows men to maintain sexual interest in their long-term partners despite the drops in testosterone that occur in conjunction with relationship entry and fatherhood.

Reactive Testosterone Responses to Social Stimuli

The changes in testosterone associated with relationship status and fatherhood concern baseline concentrations over timescales of weeks or months. Testosterone is also known to exhibit rapid changes on the timescale of minutes to hours in response to more immediate contextual triggers. In a wide range of nonhuman vertebrate species, for instance, nontactile exposure to conspecific females or their stimuli can trigger male testosterone increases within about fifteen to forty-five minutes, with testosterone concentrations usually returning to baseline within one to two hours from the onset of stimulus exposure (reviewed in Roney, 2016b). These responses are regulated by a phylogenetically conserved limbic–hypothalamic neural pathway that implements decision rules regarding the magnitude of responses (Roney, 2016b). Experimental induction of testosterone increases at timescales similar to these natural responses has been shown to promote outcomes such as reduced fear and risk aversion, increased aggression toward other males, induction of place preferences for contexts in which hormone increases occurred, reduced pain sensitivity, and reduced latency for mounting females (reviewed in Gleason et al., 2009; Muller, 2017; Roney, 2016b). Thus, in response to immediate cues of mating opportunities, short-term testosterone responses acutely prime a coordinated set of outputs that calibrate the organism toward competing for mating opportunities.

Evidence supports a phylogenetically conserved reactive testosterone response to potential mates in human males. A series of laboratory experiments has supported reactive increases in men's testosterone after brief in-person social interactions with young women that tend to be absent after brief social

interactions with young men (Kordsmeyer & Penke, 2019; Roney et al., 2003, 2007, 2010; van der Meij et al., 2008). Field studies have also provided some corroborating evidence for testosterone increases after men interact with potential mates in a range of nonlaboratory environments (Escasa et al., 2011; Flinn et al., 2012; Murcia et al., 2009; Ronay & von Hippel, 2010). The human responses exhibit various parallels with the nonhuman patterns, furthermore, including similar timescales of effects, the absence of responses after comparable social interactions with other males, and reactive increases in cortisol that co-occur with the testosterone elevations (reviewed in Roney, 2016b). Those parallels support the likelihood that homologous brain mechanisms implement the hormone responses in humans and in nonhuman species.

As in nonhuman species, evidence supports short-term testosterone increases in humans having a suite of effects that should facilitate mate competition efforts. A mix of hormone administration and correlational studies has shown that testosterone elevations may acutely reduce fear responses, increase risk-taking and reward sensitivity, increase willingness to compete with and aggress against other research participants, increase weight-lifting performance, and increase the magnitude of courtship-like behaviors directed toward young women (reviewed in Carré & Olmstead, 2015; Roney, 2016b). These outcomes collectively suggest an enhanced willingness and ability to compete for a potential mate, although the triggers of testosterone increases in these studies were not mating stimuli but instead either hormone administrations or competitive laboratory tasks. Kordesmeyer and Penke (2019), however, did assess downstream correlates of reactive testosterone responses to a series of competitions with another man that were observed by an attractive female confederate and found that the magnitude of testosterone increases correlated positively with pre/post changes in both self-reports of men's competitiveness and observers' ratings of men's self-assurance. Thus, reactive testosterone increases after exposure to potential mates may acutely intensify the orientation toward mate competition that is associated with elevated baseline testosterone concentrations in single men, thereby promoting more immediate courtship efforts.

Functional Roles of Hormones in Human Mating: Summary and Conclusions

Hormones are coordinating signals that prototypically calibrate organism-

wide responses to adaptively relevant input circumstances. Their functions are thus best understood within the context of theoretical frameworks that specify mappings from input conditions to coordinated output effects. The goal of this chapter was to lay out the broad theoretical frameworks that have organized our understanding of the role of hormones in mating psychology and behavior both in nonhuman species and in humans. The frameworks sketched are basic in many respects but can serve as organizing foundations, additions to which can help construct more complete models of the endocrine regulation of human mating.

Hormones play crucial and well-established organizational roles in the development of sex-differentiated phenotypes and behavioral strategies in many nonhuman species. In humans, converging lines of evidence support prenatal androgen signaling and the canalization of androgen effects as important causal factors in the development of sexual orientation. In principle, other individual differences in mating psychology could be traceable to quantitative differences in early androgen exposure, although the relevant pathways are complex and some influences, such as epi-marks, are very difficult to measure. Progress in mapping organizational effects of hormones to individual differences in adult mating psychology may require improved abilities to measure the magnitude of early androgen signaling.

In females of many nonhuman species, estradiol and progesterone act as a simple, two-signal endocrine code that causes shifts in motivational priorities based on temporal fluctuations in fecundity. Recent evidence supports the conservation of the priority-shifting effects of these hormones in humans, with the two-signal code having opposite effects on sexual versus feeding motivation. Pair-bonding in humans may have caused important changes in these hormone effects, however, such as a weakening of hormonal versus social influences on sexual motivation to facilitate an expansion of nonconceptive sexuality. Likewise, effects of progesterone on female odors that are seen in nonhuman species may have been suppressed in humans as a means of concealing ovulatory timing. Future research on the endocrine predictors of variables like odor attractiveness can test whether and how cues of ovulatory timing have been concealed in humans, thus potentially contributing important evidence regarding the evolution of human pair-bonding.

Versions of dual sexuality theory have argued that ovarian hormones primarily affect women’s mate preferences rather than shifts in more general motivational priorities. The infidelity-based mixed-mating hypothesis should predict strong inhibitory effects of progesterone on women’s preferences for masculine traits in men given that an infidelity cannot reap genetic benefits

during the nonfecund luteal phase when progesterone is elevated. Yet, a series of recent studies have produced null findings for within-women correlations between fluctuations in progesterone and changes in attraction to masculine traits. These findings are still being actively debated, however, and further research may be necessary to reach more definitive conclusions regarding the role of ovarian hormones in women's mate preferences.

The challenge hypothesis has organized many findings on testosterone fluctuations and their effects in nonhuman species. Human males conform to the same basic patterns predicted by this hypothesis. Men's testosterone drops after relationship entry and during fatherhood, and evidence supports a psychological orientation toward mate-seeking as a key variable in these shifts. Further, more immediate social stimuli suggestive of mating opportunities and mate competition can prime rapid, reactive increases in testosterone that may more acutely prime an orientation toward courtship efforts. All of these patterns fit within theoretical frameworks that also incorporate more somatic and physiological effects of testosterone (see fig. 29.1).

Although the frameworks proposed here for ovarian hormones and testosterone may be foundational for understanding the roles of these hormones in human mating, they are nonetheless surely incomplete accounts of endocrine influences on human mating. An important extension of these arguments concerns the roles of other hormones and how they interact with the gonadal hormones profiled here in what may comprise complex endocrine codes indexing specific, adaptively relevant input conditions. As a hint of this complexity, oxytocin production and receptor expression are partly regulated by estradiol (see Shukovski et al., 1989), which raises possibilities for these two hormones jointly affecting variables like sexual desire or relationship intimacy in interactive ways. Likewise, although testosterone responses to social interactions with potential mates may prime outputs that promote possible mate competition, the importance of pair-bonding in human mating raises the possibility that other hormonal signals may play important roles in early responses to potential mates. In prairie voles, for instance, oxytocin (Williams et al., 1994) and corticosterone (DeVries et al., 1996) are casually implicated in the formation of pair-bonds, raising the possibility that reactive changes in these hormones may be part of an endocrine cascade that initiates the pair-bonding process in humans. Research that investigates possible multisignal endocrine codes implicated in human mating may importantly supplement the theoretical frameworks proposed here, and represents an exciting direction for future research in human behavioral endocrinology more generally.

Notes

1. Gangestad et al. (this volume) devote an entire paragraph to arguing that I have mischaracterized the hormonal predictors of nonhuman primate sexual motivation in Roney (2018) and in this volume. They cite evidence that chimpanzee females may initiate more total copulations on days with lower conception probability than on days with maximum fecundity (when they are more likely to resist all but the most dominant males), and they conclude from this that "chimpanzee sexual motivation does not follow the patterns of hormonal inputs proposed by Roney (2018)." I actually discussed the female initiation findings in Roney (2018) but argued that these patterns still occur within a broader cycle phase pattern in which sexual behavior is positively associated with estrogen production but negatively associated with progesterone concentrations. Indeed, Emery Thompson (2005) directly demonstrated in a sample of wild chimpanzees that female copulation rates peaked on the same days as the females' highest estrogen production, whereas copulations decline precipitously after luteal phase progesterone elevations produce sex skin detumescence. This is very consistent with the pattern of hormonal inputs that I have proposed. Although there are some exceptions (also cited in Roney, 2018), these hormonal predictors of female sexual behavior are found across many nonhuman primate species (see Emery Thompson, 2009; Wallen, 2013).
2. Gangestad et al. (this volume) offer lengthy critiques of motivational priorities theory in their chapter. Unfortunately, given the broader scope of this chapter (hormone effects more generally), space limitations preclude detailed responses to all of their points. Nonetheless, some clarifications are important to avoid misinterpretations. For example, Gangestad et al. criticize the notion of "general sexual desire" or "libido," and they relatedly imply that an upregulation of general desire should motivate taking any sexual opportunity. First, "general desire" has been used in explanations of motivational priorities theory to distinguish its claims from those of specific versions of dual sexuality theory (e.g., dual mating theory) in which it has been alleged that only desire for men with good genes indicators tends to increase within the fertile window, but there is nothing within motivational priorities theory that entails that desire is necessarily detached from representations of specific people. When women answer questions phrased as "desire for sexual contact," they may well be picturing contact with specific mates, and hormonal predictors of women's desire for their own long-term partners and for extra-pair men were similar to those for target-unspecified measures of desire (Roney & Simmons, 2016). Likewise, women have strong mate preferences and nothing in motivational priorities theory suggests that hormonal influences on desire would nullify those standards. This is equally true for nonhuman species for many of which it is generally accepted that female sexual receptivity is restricted to fecund time periods without entailing that females are unselective in their mate choice. In mechanistic terms, fecundity-mediated shifts in desire can be reconciled with strong mate preferences by having the neural structures that regulate sexuality be primed (or inhibited) by ovarian hormones while also requiring social stimuli of sufficient strength for their full activation (see Roney, 2018).
3. The two-input position can also help address some of the criticisms that Gangestad et al. (this volume) level against motivational priorities theory. Gangestad et al. imply, for instance, that the mechanisms posited by motivational priorities theory should have produced maladaptive outcomes by promoting sexual behavior even during cycles in which conception would not have promoted fitness (e.g., when a woman had insufficient social support). Although ovarian hormones may prime neural structures that regulate desire within the fecund regions of such cycles, other inputs are likely to have much stronger inhibitory effects on those same structures. Stress, perception of risk, poor relationship quality, and lack of relationship security may all strongly inhibit sexual desire or behavior, and these inhibitory effects are likely to be much stronger than the hormone priming effects (some evidence for this is reviewed in Roney, 2019). One possibility is that cautionary mechanisms inhibit sexual behavior early in courtship until there is sufficient relationship security to release this inhibition: if so, those inhibitory effects could entail that fecundity-related shifts in sexuality are found more clearly in partnered versus single

women, and some evidence does in fact support this pattern (Roney & Simmons, 2016).

Gangestad et al. (this volume) further suggest, however, that any such cautionary inhibition should be greater during the fertile window when conception is actually possible: in effect, that there should be hormone-mediated conception avoidance mechanisms. I think this is an interesting idea that has a clear functional logic to it, but I also see these as additional mechanisms that may be combined with those proposed by motivational priorities theory. Many different neural architectures could implement such effects. Imagine, for instance, specific neural structures that regulate desire and that have their firing thresholds modulated by ovarian hormones in the ways proposed by motivational priorities theory. Downstream of these structures may be cautionary mechanisms that have inhibitory effects on sexual behavior based on variables like relationship insecurity but that are also primed by ovarian hormones in such a way that caution is greater when fecundity is higher (in alternative architectures, such mechanisms might also be upstream of desire). Once a secure pair bond is established, though, these cautionary mechanisms lose the social inputs that cause their activation, and the proposed two-signal pattern of ovarian hormone effects on sexual motivation may then emerge more clearly. Specifying candidate neural architectures of this sort can help focus debates on empirically testable elements of mechanism design. I am attempting to use the nonhuman neuroscience literature to build models of the neural architecture that could implement the two-input pathway ideas described here, though the details of these models are beyond the scope of this chapter.

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CHAPTER
30

Understanding Women's Estrus and Extended Sexuality: The Dual Sexuality Framework

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Abstract

Women are sexually active throughout their ovarian cycles and yet sex can lead to conception only a modest proportion of the cycle. Hence, whereas some of the time, women's sex is conceptive, at other timepoints, it is nonconceptive. Most mammalian females, by contrast, are sexually active only when sex can lead to conception. Women's nonconceptive sexual proceptivity and receptivity evolved for functions other than conception itself. Form follows function. The dual sexuality framework, then, proposes that women's sexuality during phases of the cycle when conception is possible differs from their sexuality during phases when conception is not possible. This perspective puts theoretical constraints on the ways that conceptive and nonconceptive sexuality can be understood. Within these constraints, multiple, contrasting psychological designs are possible. Research that assesses alternative possible psychological designs promises to enhance our understanding of human mating in ways that extend far beyond the domain of women's phase-specific sexuality.

Key Words: menstrual cycle, ovulation, estradiol, progesterone, social endocrinology, evolutionary psychology, mating

We humans share many homologies with our fellow mammals, such as a single heart, warm-bloodedness, and mammary glands. We have also evolved a host of distinctly human features, such as unusually large brains relative to body

size, a developmentally late transition to a reproductive state, bipedalism, and substantial levels of paternal care and provisioning. Unusual features within the hominin lineage are signatures of the niche that humans evolved to occupy, distinguishing us from close relatives. These features demand our attention as we aspire to understand what it means to be human (e.g., Kaplan et al., 2000; Tooby & DeVore, 1987). One such feature is the extension of a woman's interest in sexual activity beyond a narrow window during which sex can lead to conception, to which female sexual interest is typically limited in spontaneously ovulating mammals (e.g., Alexander & Noonan, 1979; Nelson, 2000; Symons, 1979).[1]

Women are sexually active across the reproductive cycle, but not necessarily sexually responsive to precisely the same stimuli and contexts across the cycle. In this chapter, we lay out the *dual sexuality framework* for understanding women's sexuality. This framework proposes that women's sexuality during phases of the cycle when conception is possible differs from their sexuality during phases when conception is not possible. This perspective puts theoretical constraints on the ways that conceptive and nonconceptive sexuality can be understood. Within these constraints, multiple, contrasting psychological designs are possible. Research that can adjudicate between alternative possible psychological designs promises to hone our understanding of human mating in ways that extend far beyond the domain of women's phase-specific sexuality.

The Dual Sexuality Framework

During approximately the first twelve days of a woman's cycle, levels of estradiol increase and an oocyte undergoes meiotic division to produce an ootid. After levels of luteinizing hormone surge and levels of estradiol begin to fall, the egg cell is released to travel down the fallopian tube. Surviving sperm in a woman's reproductive tract have a chance to meet the egg cell at this time and join to create a zygote, and ultimately an offspring. The window during which sex (and insemination) can produce these dramatic consequences is referred to as the *periovulatory (conceptive) phase*. In women, this window typically lasts about five days (out of a twenty-eight-day cycle), ending on the day of ovulation itself (Dunson et al., 2001).

Estrus and Extended Sexuality

In many mammalian species with spontaneous ovulatory cycles, females are sexually active only during the periovulatory phase. In the late 1800s, this phase

was dubbed *estrus*, from the Greek word for the frenzy that certain mammals exhibit when botfly eggs burrow into their skin and irritate their tissues). An adaptationist view (focusing on evolved function) readily explains why sex should be constrained to estrus if the sole function of sex is to directly result in reproduction. Sex outside estrus cannot lead to conception, and sex is not cost free (minimally, it entails opportunity costs). Therefore, selection should favor sex only when conception is possible.

Yet many species engage in sexual activity outside the periovulatory phase, a phenomenon known as *extended sexuality* (Rodriguez-Girones & Enquist, 2001). This term denotes the fact that female sexual activity has evolved to temporally extend beyond the narrow conceptive window of the cycle. It need not span the entire cycle, and in most instances, it extends to a portion of the nonconceptive phases. However, human females are exceptional in that sexuality extends across all cycle phases and during nonreproductive periods, such as pregnancy.

Based on the evolutionary logic outlined above, extended sexuality should evolve only when its fitness benefits exceed the costs of sex. These benefits cannot be conception, so what possibilities remain? Different benefits are possible across species. Benefits that selected for extended sexuality in one species need not be the selective benefits in another (though extended sexuality across species may be homologous and maintained by similar benefits). We emphasize that a crucial, neglected task for evolutionary scientists interested in human mating systems is to understand the fitness benefits that ancestral women gained through extended sexuality.

Dual Sexuality

Female sexual psychology does not guide women to engage in sex indiscriminately but rather to be sexually responsive to particular targets in particular contexts, as we describe below. We use the term “sexuality” as a shorthand descriptor of the psychological systems that regulate when and under which circumstances women have sex. These psychological systems include motivational and emotive processes, which recruit perceptual and cognitive processes (see Del Giudice, in press). Female sexuality encompasses the complex adaptive psychological design that impacts which targets females find sexually attractive and repulsive, when and how they act on attractions, and under what circumstances they inhibit attractions (e.g., Finkel, 2004). Sexuality influences immediate sexual responses and, also, pursuit of relationships, subsequent sexual activity, and longer-term relationships.

From an adaptationist perspective, female sexuality will be designed to elicit

fitness benefits of sex while also managing costs. In species with extended sexuality, the fitness benefits of sex varies across the cycle. Conception is a benefit (or, as we explain below, in some cases a cost) that results only from conceptive sex. Sex outside the periovulatory phase must generate other benefits. In many instances, the psychological systems that motivate sex during the periovulatory phase will differ, at least in part, from the systems that motivate sex during nonconceptive phases of the cycle. In short, females in many species with extended sexuality should possess two sexualities—a *dual sexuality* (Thornhill & Gangestad, 2008).

We refer to the sexual design shaped to regulate sex during nonconceptive phases as *extended sexuality* and the sexual design shaped to regulate sex during the periovulatory phase as *estrous sexuality* (Thornhill & Gangestad, 2008).[2] We stress that dual sexuality does *not* imply two discrete periods of sexuality. The probability of conception across the cycle is graded. In women, it is near-zero during menses, is non-zero several days prior to ovulation, peaks roughly two days before ovulation and precipitously falls immediately after ovulation (Dunson et al., 2001). Transitions between extended sexuality and estrous sexuality should be similarly graded. Dual sexuality does not imply zero overlap in the psychological systems that govern sexual interactions or the functions they serve. Interactions outside estrus can affect subsequent interactions during estrus and thereby *indirectly* influence reproduction. And sex during estrus can yield benefits other than conception. Crucially, however, if specific fitness benefits or costs of sex across phases quantitatively differ, then selection should favor differences in the systems that regulate sexuality across phases.

DUAL SEXUALITY IN NONHUMAN PRIMATES

Although rare in mammals in general, most monkeys and apes possess extended sexuality (Martin, 2007). For instance, female chimpanzees have sex on approximately ten days in a thirty-day cycle, but sex can lead to conception on just two or three of those days (e.g., Stumpf & Boesch, 2005). Females in most cercopithecine monkey species (e.g., baboons, macaques, and mandrills) exhibit at least several days of extended sexuality; those in at least one species, Assamese macaques, are sexually active almost the entire cycle (Fürtbauer et al., 2011). In some species, females rarely initiate sex outside the periovulatory phase but might still acquiesce to male advances when resistance costs more than nonconceptive sex (e.g., rhesus macaques; Dixson, 2012). In other species, females actively seek nonconceptive sex. For example, black capuchin females resist submissive males during the periovulatory phase but actively initiate sex with them during the luteal phase (Dixson, 2012).

In primates living in multimale groups in which males may harm offspring they "know" are not their own, promiscuous female mating may function to "confuse paternity"—by not allowing resident males to eliminate the possibility that offspring are their own (Hrdy, 1979; Van Schaik et al., 2000). In these species, females can broadly confuse paternity during a phase of extended sexuality and still retain the ability to choose a desired sire during the estrous phase, either for genetic benefits (e.g., Nunn, 1999) or paternal protection (e.g., Alberts & Fitzpatrick, 2012). Thus, females in species that have a functional period of extended sexuality possess a dual sexuality (Van Schaik et al., 2000; see also Rooker & Gavrilets, 2020). (For empirically investigated examples, see Heistermann et al., 2001 (Hanuman langurs); Lu et al., 2012 (Phayre's leaf monkeys); Knott et al., 2010 (orangutans); Tiddi et al., 2015 (black capuchins); Matsumoto-Oda, 1999; Stumpf & Boesch, 2005 (chimpanzees; but see also Muller et al., 2011)).

We emphasize four points about this particular form of extended sexuality in nonhuman primates.

1. Female extended sexuality is designed to influence male behavior, though, in theory, it could evolve through effects on female behavior. Harm reduction to offspring is a major fitness benefit for females, though not the only possible benefit of extended sexuality (see below).
2. Extended sexuality for this benefit can evolve only because males cannot perfectly discern when females are conceptive. Many promiscuously mating primate females also possess sexual swellings. Crucially, these swellings do not perfectly advertise conceptive status (Nunn, 1999; also Rooker & Gavrilets, 2018). If sexual swellings provided perfectly reliable cues of conceptive status, males would evolve to be disinterested in females they "know" are nonconceptive.
3. Females efficiently gain the benefit of reduced harm to offspring while preserving choice in paternity *because* sex during extended sexuality is nonconceptive. By having nonconceptive sex with males that they do not wish to father their offspring, females can effectively confuse paternity. Selection, then, shaped female preferences to vary across conceptive and nonconceptive phases. Females should prefer to have sex with males they do not wish to father their offspring relatively more during extended sexuality.
4. In theory, females could be *more* sexually active during extended sexuality than during estrus. Stumpf and Boesch (2005) found that chimpanzee females solicit sex from *more* males and are *less* likely to resist sexual advances of males (especially males not preferred as sires) during extended sexuality than during estrus.

WOMEN'S EXTENDED SEXUALITY

To evolve and be maintained, women's extended sexuality must also afford special benefits. Paternity confusion, however, is an unlikely function. As pair-bonding and biparental care purportedly evolved in humans, females should have evolved to generally assure paternity of primary partners (e.g., Gavrilets, 2012). Symons (1979) and Alexander and Noonan (1979) proposed alternative functions: that women's extended sexuality evolved (at least in part) to enhance

pair-bonding and bolster male investment in offspring. Later, we flesh out one scenario along these lines and discuss other possible functions of women's extended sexuality (see section "Extended Sexuality").

HORMONAL UNDERPINNINGS OF ESTROUS AND EXTENDED SEXUALITY

Selection should have shaped female sexuality to be contingent on cycle phase by crafting proximate psychological processes that track conception probability. Ovarian hormones—estrogens and progesterone—regulate women's fecundity (and, more broadly, those of female mammals; e.g., Ellison, 2001). Roney (this volume) argues that a "two-signal" endocrine code regulates women's sexual interests across the cycle. The dual sexuality framework shares this view, though our perspective departs considerably from Roney's for understanding the outcomes it produces (see below). In many, if not all, cases, estradiol and progesterone have opposing effects: estradiol upregulates estrous sexuality and suppresses extended sexuality, while progesterone upregulates extended sexuality and suppresses estrous sexuality. Increasingly, investigations of psychological shifts across the cycle seek to understand how estradiol and progesterone affect behavior.

Figure 30.1 represents how cyclic variations in estradiol and progesterone may affect estrous and extended sexualities.

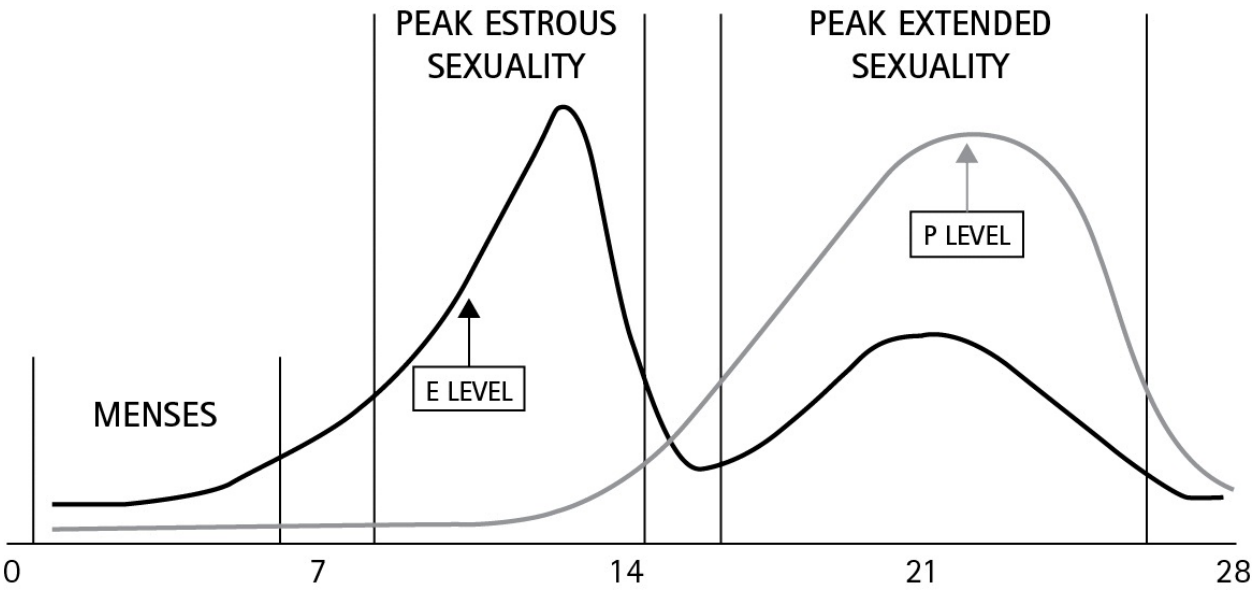

Figure 30.1 Idealized representation of estrous sexuality and extended sexuality. Relative (not absolute) levels of estradiol (E) that exceed relative levels of progesterone (P) support estrous sexuality; relative levels of progesterone that exceed relative levels of estradiol support extended sexuality. The figure shows idealized peak phases of estrus and extended sexuality in an average cycle (day of ovulation = day 14). Days of the cycle outside of these peaks are transition phases, intermediate phases, or menstrual days. In

reality, hormonal underpinnings could be more complicated (e.g., hormones may have delayed effects by influencing receptor concentrations; e.g., Roney & Simmons, 2013). But most hormonal studies largely examine simple additive effects of current levels on behavioral outcomes.

Estrous Sexuality: Conceptual Considerations

To predict differences across phases or hormone effects on sexuality, we need some idea of the special benefits and costs of estrous and extended sexuality. We begin with estrous sexuality.

FUNDAMENTAL INSIGHTS INTO FEMALE ESTROUS SEXUALITY

The distinct element of estrous sexuality is seemingly simple: sex during estrus can ultimately result in the birth of an offspring, a momentous event in the life history of women. If the pregnancy is successful, a mother will nurture an offspring through nine months of gestation and many more months of lactation —in foraging societies, two + years of supplying the offspring with 100 percent of its nutritional needs. For many more years thereafter, the offspring will depend on partial dietary subsidization and demand protection and other investments (e.g., teaching; Kaplan et al., 2000). Fathers, kin, and a broader social network will substantially contribute to raising the offspring (e.g., Hrdy, 2009; Kaplan et al., 2000). Yet, at least through gestation and lactation, others' provisioning flows through a mother's body. The tremendous time and effort women commit to gestating, lactating, and caring for an offspring represent massive opportunity costs; that time and effort could have been dedicated to producing and supporting different offspring.

Men may also dedicate a good deal of effort to caring for offspring. But a key difference is that men are not obligated to care for offspring to reproduce; they need only have a single sexual encounter with a female. Trivers (1972) offered fundamental insights into male and female roles in sexual selection when these asymmetries in obligatory parental investment exist, as is true in mammals. Males should be selected to seek out and accept sexual opportunities with conceptive females. Females, then, typically need not work hard to have an abundance of sex partner options available to them. Because males willing to have sex with females are typically not in short supply, neither is sperm that females require to conceive an offspring.

At the same time, the partner options that females have to choose among do not equally enhance their fitness. In 90 to 95 percent of mammalian species, males do not care for offspring (e.g., Woodroffe & Vincent, 1994), and, hence, the important differences between males largely consist of differences between the fitness value of genes they give to offspring (e.g., the extent to which they

carry deleterious mutations). In some species, including humans, males care for offspring. Therefore, partner options also differ in male willingness and ability to enhance offspring fitness or quantity through paternal provisioning or care. Although women could have conceptive sex with any one of many potential partners, the vast majority of their options are very poor. Most have low genetic quality, relative to the best potential partners. Although high-quality paternal investment can readily compensate for poorer genetic contributions to offspring, males also differ with respect to their ability and willingness to invest in a particular female's offspring. High-quality paternal investment is limited and likely not freely offered. And in light of the limited number of offspring that women can rear in their lifetimes, given the massive time and energy costs dedicated to each one, even a single poor reproductive choice can have large fitness consequences.

A key to understanding the design of women's estrous sexuality follows: Women should be strongly selected to *wisely* utilize their limited reproductive opportunities and choose among potential partners. On some occasions—perhaps many—women's most adaptive decision is to delay reproduction at least one cycle.

A key question is precisely what constitutes a "wise" choice. Here, wisdom hinges on the selective contingencies operating ancestrally: the fitness value of male investments; the likelihood of male investment contingent on circumstances; the value of cooperative care from kin networks; the value of male genetic benefits; the ways in which fitness benefits are moderated by context and life histories; and so on. The strength and form of historical selection constraints are uncertain—and debated, as we later discuss. As a result, the seemingly simple distinct element of estrus—sex can result in conception—generates a challenging scientific puzzle. Within the constraints of the dual sexuality framework, specific selection scenarios can guide empirical explorations of the design space of estrous sexuality (e.g., Durante et al., 2016). Designs found to exist constitute footprints of important selective forces that shaped human mating and reproduction (e.g., Haselton, 2018; Thornhill & Gangestad, 2008; Tooby & Cosmides, 1992).

A CONTRASTING PERSPECTIVE: MOTIVATIONAL PRIORITIES

The dual sexuality framework can be contrasted with an alternative view, motivational priorities theory (Roney, 2018, this volume; Roney & Simmons, 2016). The views begin with the same observation: Only during estrus can sex lead to conception. But from this point, the perspectives diverge. Motivational priorities theory views conception as a benefit. Nonconceptive sex also offers

benefits. But due to the unique benefit of conception, sex during estrus has historically been more beneficial than sex outside estrus. Accordingly, selection led to a simple quantitative difference in general sexual desire between estrous sexuality and extended sexuality. In the words of Roney (2018), "The main function of estrus is to shift motivational priorities toward sexual behavior when conception provides a fitness benefit" (p. 246). Because sexual motivation trades off with other pursuits, other motivational differences exist, notably appetite. Hormones regulate this trade-off: Estradiol enhances sexual desire and suppresses appetite; progesterone has the opposite effects.

Naturally, women differentially evaluate their mating options. Some men are more attractive than others. Primary romantic partners may be especially attractive. In motivational priorities theory, however, hormones do not selectively affect the attractiveness of targets. Metaphorically, hormones regulate sexual desire in the way that a stereo system's volume control knob regulates sound output. A clockwise turn of the knob increases the amplitude of all frequencies; analogously, rising estradiol levels and falling progesterone levels purportedly increase the sexual value of all male targets. A metaphorical counterclockwise turn—falling estradiol levels and rising progesterone levels—diminishes the sexual value of all male targets.

Motivational priorities theory recognizes that social "inputs" affect sexual desire too, often for specific targets. But these impacts are independent of hormones. If a romantically involved woman engages in sex to deepen intimacy with her partner, while another woman less interested in her partner does not desire sex for greater intimacy, we should expect the two women to constantly differ in their levels of sexual desire across the cycle. Both women should still experience a relative increase in sexual desire during estrus. Put otherwise, hormonal and social impacts on sexual desire are additive, not interactive (Roney, 2018).

Based on conceptual considerations discussed above, we question two primary assertions of motivational priorities theory: that conception is likely always a benefit (at least on average ancestrally, when women are physiologically capable), and that estrous sexuality is characterized by an increase in general sexual desire.

CONCEPTION IS NOT ALWAYS A BENEFIT

We argued that selection should have shaped women's adaptations to wisely choose among options to conceive during estrous sexuality. Conception might nearly always be beneficial relative to *never* conceiving. But the choice women face is between conceiving now and conceiving at least one cycle later. In many

circumstances, conceiving now is a worse choice. Consider four women in context:

1. A single, unpartnered woman who has no partner on whom she can rely
2. A partnered woman who questions whether her partner is “Mr. Right”
3. A partnered woman passionately in love with her partner, but whose relationship has yet to fully solidify
4. A partnered woman exceptionally well bonded with her partner, as she evaluates him to be a dedicated father-to-be, who is fully committed to her and a sufficiently fit sire

Does conception during the current cycle enhance the fitness of all four? Motivational priorities theory implies yes. By contrast, dual sexuality framework recognizes that, under systematic circumstances, current reproduction reduces fitness, relative to waiting. If cues, recurrent over evolutionary time, index those circumstances, women’s estrous sexual interests should be sensitive to those cues.

ON THE CONCEPT OF GENERAL SEXUAL DESIRE

Roney and Simmons (2013) sought to examine “physiological signals [hormones] that regulate cyclic patterns of libido” (p. 636). Freud (1953) introduced the concept of libido: “The fact of the existence of sexual needs in human beings and animals is expressed in biology by the assumption of a ‘sexual instinct,’ on the analogy of the instinct of nutrition, that is of hunger. Everyday language possesses no counterpart to the word ‘hunger,’ but science makes use of the word ‘libido’ for that purpose” (p. 135). One need not accept Freud’s psychoanalytic explication of libido to appreciate the fundamental premise here: Libido is an internally generated energy (drive or “Trieb”) that motivates sex. Indeed, Roney (2018) too compared sexual desire to appetite.

Libido is conceptualized as a general desire for sex that it is not specific to particular targets. As Fisher (1998) described, “The sex drive (the libido, or lust) is characterized by the craving for sexual gratification; it is associated primarily with the estrogens and androgens; and it evolved primarily to motivate individuals to seek sexual union with any conspecific” (p. 24). The notion is akin to hunger: When hungry, general cravings for food motivate consumption; some foods may be preferred but, if preferred foods are not available, less preferred foods are often (though not always) still beneficial to consume. However, there are two separate pieces of sexual interest (and hunger): what/whom someone is specifically interested in, and how intensely someone experiences interest. When we talk about “general (nonspecific) sexual desire,” these two concepts are conflated. If someone is experiencing heightened sexual interest, does that mean

that they are experiencing both a greater intensity of interest and an interest in more individuals? (For a contrasting view of sexual desire, see Toates, 2009, 2014).

Probably not—at least in the case of women who ovulate. As we emphasized, it makes little sense that conceptive women would benefit from having sex with (and hence carrying the offspring of) *any* male. If a preferred partner is not currently available, it is likely *not* beneficial to conceive with the next available partner. Not only is producing and rearing a child costly, reproducing with a nonpreferred partner can reduce the likelihood of ever forming—and reproducing within—a long-term pair-bond with a highly preferred partner. Conceptive sexual interests should be highly discriminating.

Hormones may affect sexual desires by modulating the targets of desire: They moderate the potential for a particular stimulus feature to evoke sexual interest within a particular context (e.g., when conceptive vs. not). Certain targets or mate features may evoke increased intensity of sexual interest under specific hormonal influences, leading to an apparent increase in sexual desire *on average*. Importantly, however, an average increase in sexual desire is not equivalent to an increase in *general, nonspecific* sexual desire. Women may feel more sexual and seek out potential mates, engage in sexual fantasy, and so on, more so than other times—but strong sexual interest in particular targets may be accompanied by strong sexual aversion to other targets.

In some instances, hormonal influences during estrous and extended sexuality may evoke different mate preferences, for different functional reasons. For example, female chimpanzees seek out sex with certain males during extended sexuality; yet females actively resist solicitations from these same males during estrus, while preferring other males. Women too may prefer sex under different circumstances during extended sexuality and estrus. This broad view of sexual desire is compatible with the dual sexuality framework but not with the concept of libido posited by motivational priorities theory.

SUMMARY

During the estrous phase, women have a multitude of available mating options. But over their lifetimes, they have limited reproductive opportunities. Selection should favor estrous strategies for choosing among options that use scarce reproductive opportunities wisely. At times, the best choice is to delay conception at least one cycle. A simple upregulation of general sexual desire when women are conceptive does not effectively solve estrous women’s adaptive problems.

Estrous Sexuality: Empirical Research

We now turn to empirical research programs, typically studies of Western populations that address questions about how women's estrous sexuality has been designed to regulate sexual interests and behavior. If estrous sexuality and extended sexuality differ, then at least some subset of potential sexual targets will elicit sexual interests differently, depending on the hormones that modulate women's dual sexualities. The defining feature of estrous sexuality is that sex can lead to conception. This unique benefit, and cost, constrains the design of estrous sexuality—such as entailing that women's sexuality during estrus should have been shaped by selection to facilitate wise reproductive choices, including the choice to delay reproduction under certain circumstances.

FERTILITY REGULATION

Based on data from noncontracepting societies, it is estimated that ancestral women typically experienced fewer than one hundred cycles in a lifetime (Strassmann, 1999), a proportion of which are anovulatory. Although each fecund menstrual cycle may provide a different opportunity for potential conception, women can only successfully rear a limited number of offspring in their lifetime. Women should therefore have adaptations that discern when and under what circumstances to optimally reproduce. Indeed, biologists have long recognized the fundamental trade-off between current and future reproduction. Reproducing too early can have fitness costs, including greater risks of infant mortality and less fit offspring (e.g., Charnov, 1991). Delaying reproduction also entails costs; the longer the delay, the more reproductive opportunities are missed. Accordingly, selection should have shaped fertility-regulation systems that adaptively calibrate reproductive decisions to environmental conditions.

Physiological Fertility-Regulation Mechanisms

Women have physiological adaptations to prevent or delay reproduction when the fitness costs of reproducing at present likely exceed the costs of waiting. Some responses are well established: Women experiencing low energy balance or high energy expenditure produce relatively low levels of ovarian estradiol and progesterone, which result in lower rates of ovulation, conception, and successful implantation (Ellison, 2001). Given the high energy demands of gestation and lactation, energetic stress likely reduced offspring survival and success ancestrally, while also threatening maternal health. Indeed, the adaptations surrounding lactation also modulate allocation of maternal resources across current and future reproduction. For instance, breast milk production and

energy content are relatively buffered from current (even severe) deficits in maternal caloric intake. This is reflective of prior investments in maternal energy stores for reproduction, as well as current metabolic investments in the offspring, at a cost to allocations toward a new pregnancy (Ellison, 2003). Lactation temporarily delays a next pregnancy, which could interfere with optimal allocation of resources to a newborn. Nipple stimulation from nursing suppresses GnRH secretion, thereby preventing the luteinizing hormone (LH) surge and ovulation (McNeilly, 2001). Current maternal energy balance also importantly determines the resumption of postpartum cycling (Peng et al., 1999; Valeggia & Ellison, 2009).

Variations in social and individual circumstances also influence the relative value of current versus future reproduction and, thus, may similarly serve as inputs into fertility-regulation adaptations. Social stressors appear to disrupt female reproductive functioning across a wide range of social mammals (Wasser & Barash, 1983). In nonhuman primates, intimidation and harassment from female group members are associated with suppressed ovarian hormone levels and ovulation failure in females who are the targets of aggression (Sapolsky, 2011; Wasser & Starling, 1988). Although empirical investigation in humans is limited, a few studies provide potential insights. For instance, one within-subjects study comparing daily hormone levels across two cycles found that psychosocial stress was associated with reductions in women's estradiol levels throughout the cycle, with the most pronounced drop occurring during the periovulatory phase (Roney & Simmons, 2015). Another study experimentally tested whether social ostracism impacts endocrine markers of fecundity. As social support was likely crucial to aid women in caring for heavily dependent offspring, women lacking reliable sources of support were hypothesized to downregulate their fecundity in response to social ostracism (Dinh et al., 2021). Results showed that following social exclusion (n = 88), versus inclusion (n = 81), by female peers, women with low levels of background daily social support experienced increases in periovulatory-phase levels of progesterone. Progesterone released by the adrenal glands during the periovulatory phase can impair follicle growth and inhibit ovulation (reviewed in Dinh et al., 2021). Progesterone increases following social exclusion, then, were consistent with potentially reduced fecundity.

Psychological Fertility-Regulation Mechanisms

Endocrine mechanisms associated with reduced or heightened fecundity may potentiate or interact with psychological mechanisms to adaptively regulate fertility. Differential costs and benefits of various reproductive decisions should

have selected for adaptations that produce condition-dependent changes in women's estrous sexual motivations.

One condition that may reduce the benefits of delaying reproduction, all else equal, is environments associated with childhood adversity, which may provide cues of elevated and less controllable mortality risk. Adverse conditions may affect age at menarche (Ellis, 2004). But once reproductive maturity is attained, women should still adaptively regulate their fertility. Women's fertility-regulation systems may calibrate estrous sexual motivations to achieve adaptive fertility outcomes, contingent on childhood conditions and other fitness-relevant cues.

In a study of more than a thousand naturally cycling, partnered women, exposure to childhood adversity moderated the impact of conception probability on women's sexual motivations (Dinh et al., 2017). Women from adverse childhood backgrounds experienced more sexual attraction to their partners and initiated sex more frequently during estrus than during extended sexuality. Women from low-adversity childhood backgrounds showed the opposite pattern: lower in-pair sexual attraction and sexual initiation during estrus than extended sexuality, particularly when relationships were relatively new. As a result, women from high-adversity backgrounds initiated more sex than women from low-adversity backgrounds during estrus but not during extended sexuality. Male partner commitment and investment are likely less certain at early stages of a relationship, and women may benefit from avoiding conception. Yet women from harsh childhood backgrounds that portend short lifespans may pay larger costs by delaying reproduction (including failure to reproduce at all) and therefore require less commitment from a partner before engaging in conceptive sex. Effects in the study were specific to in-pair sexual interests. There were no childhood environments × conceptive status interaction effects predicting sexual interests in extra-pair men.

These studies support the logic that not every conceptive phase optimally results in conception. Fitness benefits, compared to costs, of reproduction depend on the contexts in which the offspring is produced. Importantly, these are only three studies, and they require replication and extension. In addition to replicating these effects, future research can also examine other possible inputs that regulate fertility, such as relationship status, male partner investment, and familial support.

OVULATORY PREFERENCE SHIFTS

The most thoroughly investigated set of hypotheses that fall under the umbrella of the dual sexuality framework concerns shifts in women's

preferences for putative indicators of "genetic quality" in men. A woman might prefer traits that indicate (albeit indirectly) the genetic fitness benefits that a man could potentially pass to her offspring.

Dual Sexuality and Preference Shifts in Historical Perspective

Much of the reason for this emphasis is historical. Even before the dual sexuality framework was applied to humans, researchers had examined some preference shifts across the cycle. Three studies assessed shifts across conceptive and nonconceptive phases in evaluations of men's scents, in relation to men's bodily symmetry (Gangestad & Thornhill, 1998; Rikowski & Grammar, 1999; Thornhill & Gangestad, 1999). Over the next few years, researchers documented similar shifts in preferences for facial masculinity (e.g., Penton-Voak et al., 1999), masculine vocal pitch (e.g., Feinberg, 2006; Puts, 2005, 2006), behavioral dominance or confidence (e.g., Gangestad et al., 2004, 2007), and bodily masculinity (e.g., Little et al., 2007). Concurrently, scholars sought to understand preference shifts in broader theoretical contexts. Pillsworth and Haselton (2006b) proposed the theory that, while conceptive, women whose primary partners lack indicators of genetic quality may be more willing to have extra-pair sex with men who do possess these indicators. Women can thus retain their relationship with their primary partner, while mating outside the relationship during estrus to secure genetic benefits for offspring (a "dual mating" strategy; see also Gangestad et al., 2002).

Thornhill and Gangestad (2008) situated these findings in a broader, cross-species framework and introduced the notion of dual sexuality. They discussed two important elements. First, previous research had largely treated nonconceptive sex as a theoretically unexamined backdrop against which to compare estrous sexuality, whereas dual sexuality demands an adaptationist account for extended sexuality. Second, estrous sexuality is phylogenetically older, with some homologies broadly shared with mammals. Whereas previous theories proposed that women's estrous sexuality evolved in the context of pair-bonding (e.g., as extra-pair sex adaptations), the dual sexuality framework emphasized that estrus-phase preferences for male features of genetic quality may be phylogenetic old adaptations that evolved in deep evolutionary time—not in the context of pair-bonding or paternal investment. Hence, shifts in preferences for putative indicators of genetic quality may *not* be part of an adaptive extra-pair mating strategy. In theory, preference shifts that facilitate extra-pair mating could have been selected *against* in the context of paternal investment and, hence, become weak and vestigial (Gangestad & Garver-Apgar, 2013; Gangestad et al., 2015; Haselton, 2018). A dual sexuality framework is

compatible with dual mating strategies but *does not entail* them.

Thornhill and Gangestad (2008) sought to situate a growing literature on preference shifts under a broader theoretical umbrella. In doing so, they heavily discussed estrous preferences for indicators of genetic quality in a broader comparative framework. Importantly, they stressed that in-pair romantic partners should often be the preferred sire, independent of their genetic qualities, because of the resource and fitness benefits that a romantic partner can offer over and above genetic benefits. Estrous sexuality should be designed to value conception in high-quality relationships with valuable romantic partners. Gangestad et al. (2015) listed multiple scenarios under which estrous sexuality has been modified in the context of pair-bonding. For instance, women in strong pair-bonds should be especially drawn to romantic partners during estrus, while suppressing extra-pair interests. Along these lines, Durante et al. (2016) conceptualized multiple possibilities within a dual sexuality framework and set an agenda for future research.

Some scholars tend to conflate the dual sexuality framework with the idea that estrus is *defined by* preference shifts for genetic quality indicators (e.g., Roney, this volume; Stern & Penke, this volume; see also Jones et al., 2018a; Shimoda et al., 2018), rather than recognizing that these preference shifts are one of many possible effects under the framework. Roney (this volume) and Stern and Penke (this volume) exclusively contrast preference shifts for genetic quality indicators with motivational priorities theory. Without recognizing the broader theory and the nuances offered by the dual sexuality framework, these authors reduce theoretical and empirical debate on women's sexuality into whether estrus shifts general sexual motivations, versus whether estrus shifts preferences for genetic quality indicators (and away from primary partners). We offer this historical backdrop as a contrast to these views.

Empirical Status of Preference Shifts for Putative Indicators of Genetic Quality

Repeated findings through the first decade of this century apparently show that preferences across multiple male features shift across the cycle, purportedly as a function of estradiol and/or progesterone levels. Now, it seems apparent that early claims were too bullish. Preference shifts appear to be relatively weak overall, limited to specific male traits, and/or conditional.

In 2014, two meta-analyses of the preference shift literature were published. Gildersleeve et al. (2014a) conducted nested analyses that included a broad or more focused set of studies. The focused analysis included studies of only of "revealed" preferences—studies that presented women with an array of variants of a male feature (e.g., scents on t-shirts supplied by men varying in symmetry

and faces in an array that vary in masculinity). The broader set of studies included studies assessing women's hypothetical ratings of male features (e.g., on Likert scales). Although Gildersleeve et al. (2014a) argued that the focused analysis was a more appropriate test of the ovulatory shift hypothesis, in both the broad and focused analyses, there were small but reliable upward preference shifts on conceptive relative to nonconceptive days across all male trait categories (e.g., facial masculinity, body masculinity, and vocal masculinity).

By contrast, Wood et al. (2014) did not reject the null hypothesis, based on an analysis that did not distinguish between studies of stated or revealed preferences. Gildersleeve et al. (2014b) pointed to a number of additional differences between the meta-analyses that account for differences in the results (see their paper for details).

Though both meta-analyses included unpublished data, effect size estimates could be inflated by publication bias and *p*-hacking (performing multiple analyses to test an hypothesis but selectively reporting those that yield $p < 0.05$; Simmons et al., 2011) To examine this, Gildersleeve et al. (2014b) conducted a *p*-curve analysis (Simonsohn et al., 2014a,b). If true effects exist, *p*-values less than 0.05 will not be equally distributed across the range; most values will fall closer to.00 than 0.05 (i.e., the distribution will be "right-skewed"). Gildersleeve et al. (2014b) conducted extensive robustness analyses using the different inclusion criteria of the meta-analyses. In eleven of the twelve *p*-curves they examined, the distribution was significantly right skewed (*p*'s ranging from $p < .0001$ to 0.03); the remaining analysis produced a $p = 0.08$ (see Gildersleeve et al, 2014b; also see Gildersleeve et al., 2017). Subsequent analyses using *p*-curve and other selection models (which could include $p > 0.05$; McShane et al., 2016) yielded results consistent with meaningful shifts in preferences for behavioral dominance/confidence/charisma, bodily muscularity, and vocal pitch, though all estimates were based on small numbers of studies and hence results were far from conclusive. At the same time, evidence weighed against notable shifts in preferences for facial masculinity, the feature examined in the largest number of studies (Gangestad et al., 2022).

In light of contrasting results, a number of research teams have sought to assess the replicability of key findings in reasonably high-powered studies. Results have been mixed, though findings have been more negative than positive.

Studies have largely been inconsistent with the facial masculinity effect. Two studies did not detect associations of within-woman variations in ovarian hormone levels and preferences for facial masculinity (Jones et al., 2018c; Marcinkowska et al., 2018). In another set of findings, one study found an

association consistent with the preference shift but the other did not (Dixson et al., 2018).

One research team reported a null association between conceptive status and preferences for body masculinity—a composite of six features (Jünger et al., 2018a). Another research team proposed that only a subset of these features qualified as indicators of upper-body strength; they found evidence in the original data consistent with negative effects of women's progesterone levels on preferences for male muscularity, in partnered but not single women (Gangestad et al., 2019a, 2019b; see also Marcinkowska et al., 2018).[3] A follow-up study and yet another study, using methods similar to Jünger et al., (2018a) yielded mixed evidence for overall effects, but found little support for moderation by partnership status (Stern et al., 2021). Yet evidence generally consistent with overall negative effects of progesterone levels on preferences for male muscularity emerged (Dinh et al., 2022b).

One study found a significant positive association between estradiol levels and preference for low male voice pitch (Jones et al., 2018d); two other studies detected no shift in preferences for either masculine pitch or formant frequency (Jünger et al., 2018b). Finally, another recent study detected no shift in preferences for behavioral dominance or confidence (Stern et al., 2020).

What, then, can be concluded at this point in time? In our view, uniform null hypotheses, across all preferences, are unlikely. One cannot simply ignore *p*-curve analyses on pre-2014 studies that are incompatible with effects equal to zero. And although "significant" results in more recent studies are spotty, effects generally run in expected directions; in none of the recent replication studies does a significant effect on preferences run in the opposite direction, as might be expected to occasionally occur if population effects were truly zero. At the same time, claims based on early studies were likely too bold. If preference shifts exist, they are likely to be restricted to certain features. And even then, simple two-way interactions (e.g., hormone × trait effects on attractiveness ratings) are unlikely to be large across women in general. Below, we consider the possibility that, for some women in certain circumstances, preference shifts are meaningful.

Moderation of Extra-Pair Sexual Interests by Partner Attractiveness

In the early 2000s, while some researchers focused on documenting shifts in preferences across conceptive and nonconceptive phases, others explored the possible impacts of purported shifts on romantic relationship dynamics. Specifically, a number of researchers asked how women's partners' features affect patterns of sexual interests across the cycle. The idea was that, if women's

preferences for “sexy” features are elevated when conceptive, then women might experience a shift in attraction to extra-pair men—but only if their primary partners are relatively low in sexual attractiveness.

In contrast to the literature on preference shifts more broadly, this finding has received considerable empirical support, including in more recent replication studies. Although some studies have measured particular partner traits (developmental stability: Gangestad et al., 2005; facial masculinity: Gangestad et al., 2010), most studies have simply asked women to evaluate the sexual attractiveness of their partners (Pillsworth & Haselton, 2006a) or their short-term sexual attractiveness in contrast to their long-term partner attractiveness (e.g., Haselton & Gangestad, 2006). Larson et al. (2012) reviewed published studies (including their own): three of five analyses yielded significant moderation by partner attractiveness on extra-pair sexual interests (five of seven if moderation by partner symmetry or facial masculinity is included); in the remaining two analyses, effects were in the same direction but not significant, $p = 0.12, 0.27$.

Since that review, two additional replication studies supported the partner attractiveness moderation effect. One study tracked a relatively small sample of women ($N = 40$) through their cycle (Shimoda et al., 2018). The data showed a significant partner attractiveness × conceptive status interaction on extra-pair sexual interests, $p = 0.027$.[4]

A second study, conducted by Arslan et al. (2021), is the largest study to date examining partner attractiveness moderation effects. The daily diary study followed more than four hundred naturally cycling women for up to forty days. It included five measures of partner attractiveness, designed to comprehensively assess the different ways partner attractiveness had been measured in the past. A strength of daily diary methods is that conception probability can be measured continuously, which affords higher power than methods using discrete high- and low-conception probability windows (Gangestad et al, 2016) and does not require that large numbers of observations be discarded. In their report, Arslan et al. (2021) claimed, “we found no evidence that sexual desire shifted more strongly among women who deemed their partner less sexually attractive” (p. 428).

In fact, however, the authors made two errors in calculation of partner attractiveness that greatly affected results.[5] When errors were corrected, the five tests of partner attractiveness × conceptive status interaction effects on women’s extra-pair interests, conducted on the full sample of 400 + women, yielded p-values of (in descending order) 0.089, 0.006, 0.002, < 0.001, and < 0.001 (Gangestad & Dinh, 2021). Analyses implementing an overall composite

measure of male partner attractiveness yielded *p*-values ranging from 0.015 to < 0.001 in the sample of 400+, as well as smaller samples of 123 and 143 that met stricter criteria of inclusion. Only in poorly powered analyses involving discrete windows (Gangestad et al., 2016), in which many observations were discarded, did *p*-values generally fail to fall below 0.05. Even in these poorly powered analyses, every effect (of 20) ran in the same direction, and effect sizes were very similar to more powerful analyses yielding highly significant effects. Effect sizes were furthermore very similar to the mean effect size in previous studies, meaning that Arslan et al.'s findings were perfectly consistent with the prior literature.

Figure 30.2 presents the analysis using a composite measure of overall male partner sexual attractiveness (Gangestad & Dinh, 2021). Arslan et al. estimated the overall main effect of conception probability on extra-pair interests to be equivalent to Cohen's *d* of about 0.4—a medium effect size. For women whose partners are 1 standard deviation (SD) below the mean on attractiveness, the effect is estimated to be about 1.5 times the average—a large effect size. For women whose partners are 1 SD above the mean on attractiveness, the effect is near zero.

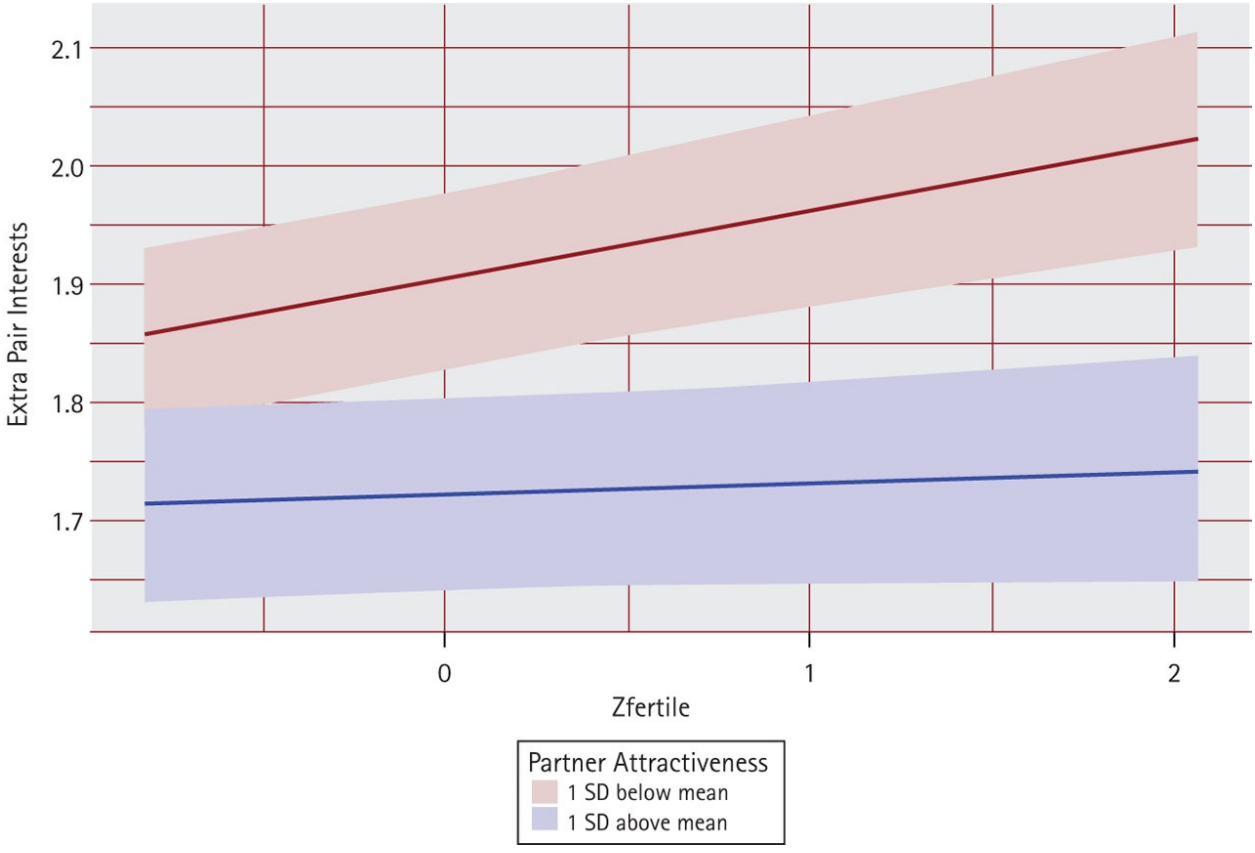

Figure 30.2 Plot of association between *z*-scored fertility (x-axis) and extra-pair sexual interests (y-axis) for women with partners 1 standard deviation below the mean on attractiveness (5-component composite measure) (red line) and for women with partners 1 standard deviation above the mean on attractiveness (blue line). Data are from Arslan et al. (in press); analyses are from Gangestad and Dinh (in press; see SOM, Figure S9). Shaded areas are 95 percent confidence intervals. Long-term attractiveness is controlled. As can be seen, the fertility effect on extra-pair interests is driven by women with partners they report to be relatively unattractive.

Two studies not yet published replicate these findings. First, Larson and Haselton (2022) found a significant partner attractiveness × conceptive status interaction, in a study of fifty-six women utilizing LH tests to confirm ovulation. Second, in a preregistered study of 180 women assessed up to four times in a cycle, Dinh et al. (2022a) found a significant partner attractiveness × progesterone interaction effect on extra-pair sexual interests: among women who rated their partner as relatively low in sexual attractiveness, low progesterone was associated with an upward shift in women's interest in extra-pair men.

In sum, evidence appears strong for partner attractiveness moderating the effects of conceptive status/hormone levels on women's extra-pair sexual interests. Even disregarding unpublished analyses, the majority of studies show moderation effects in expected directions, despite most having modest sample size. Although current data clearly indicate moderation effects of meaningful size, more data would be helpful to better assess effect size estimates.[6]

Can the Lack of Robust Preference Shifts Be Reconciled with Partner Moderation Effects?

This moderating effect of male partner attractiveness on extra-pair desires appears to be real, as detailed above. Yet clear, strong evidence for shifts in specific preferences is lacking. How, then, are these contrasting effects to be reconciled?

One possible response is to see preference shifts and moderation effects as reflections of the same phenomena and, therefore, to evaluate the strength of evidence for both based on the aggregation of studies across domains. Indeed, Roney (this volume) and Stern and Penke (this volume) do not evaluate evidence for each of these phenomena separately. Given mixed evidence across the ovulatory shifts literature, they group all ovulatory shifts together and indicate that all such effects are unlikely to be robust. However, preference shifts and moderation effects are not the same phenomena. The evidence pertaining to each needs to be evaluated on its own. Evidence favoring one effect but not strongly favoring the other presents an empirical puzzle to be explained, not dismissed.

Analyses of preference shifts have been examined across all women, and

these analyses are conceptually distinct from those of partner attractiveness moderation effects. The latter offer targeted tests, specific to women in relationships, which imply that a subset of these women drive overall effects. The former imply that all women's preference shifts should show roughly the same pattern, independent of their relationship status, background social support, physical state, and (for partnered women), characteristics of the relationship and partner. As we outlined in the introduction, this is theoretically inconsistent with parental investment theory and increasingly inconsistent with the evidence. By contrast, by their very nature, moderation effects account for variation in circumstances central to the core logic of ovulatory shifts; not all women would have benefited from conception with any given partner on any given cycle.

Empirically, for some women, hormonal effects are purportedly strong, such as effects on extra-pair interests. For other women, hormonal effects are purportedly absent (or could even run in an opposite direction). This gives rise to one possible reconciliation of the literatures: It is plausible that extra-pair interests *and* preference shifts are moderated—strong for some women, but absent (or even in the opposite direction) for others. If so, overall mean preference shifts could be very small, despite being considerable (at least in some domains) for a subset of women. Along similar lines, Durante et al. (2016) offered comparable thoughts, with respect to moderation by relationship qualities (attachment or bond strength):

> One useful metaphor is that the psychological experience of romantic attachment could act as a filter through which the cognitive and motivational outputs of ovulatory cycle adaptations pass. In principle, such a filter could reduce the strength of ovulatory shift effects. For example, although the fertile phase of the female ovulatory cycle is, on average, associated with increases in women's sexual desire for men who possess markers of genetic fitness, the fertile phase in highly bonded women might be associated with smaller (or no) increases in sexual desire for these men. (p. 29)

In principle, the same could be true of women paired with attractive partners. Or more generally, it may make sense for estrous women to differentially evaluate extra-pair men based on sexually attractive features, only when they exhibit estrous extra-pair interests. If their estrous extra-pair interests are suppressed, for adaptive reasons, women benefit little from discriminating between extra-pair men's sexiness. Of course, we do not yet know if this explanation is correct. But it has been proposed, and certainly should be evaluated.

Other resolutions are also possible. Small effects in individual preference domains could perhaps aggregate into larger effects. Preference shifts could pertain to features not yet well investigated. Perhaps partner attractiveness

moderation effects are not mediated by preference shifts (though it is not apparent what alternatives are plausible). Women's attraction to certain markers of genetic quality could be dampened when presented with strangers (as in typical lab studies), where features such as strength and dominance could be associated with threat of sexual coercion (see, e.g., Li et al., 2014). Finally, it is possible that, despite the current state of the evidence, moderation of phase or hormonal effects on extra-pair sexual interests by partner attractiveness is not real—a possibility that appears to us to be very unlikely at this point, but subject to further investigation.

SELECTIVE AVOIDANCE OF KIN AND RISK

Some scholars have proposed that, when conceptive, women should be sensitive to information about, and avoid situations associated with, unwanted sexual contact (e.g., Chavanne & Gallup, 1998). A recent meta-analysis found that women recognized cues (e.g., facial expressions) potentially associated with sexual coercion with increased sensitivity during the ovulatory phase than during the luteal phase (Boudesseul et al., 2019). Effect sizes, however, were highly heterogeneous, suggesting that effects may be specific to certain domains. Accuracy of perceiving emotional facial expression in general tends to be enhanced by estradiol and suppressed by progesterone (Osório et al., 2018).

When conceptive, women's motivations to avoid male kin (and therefore avoid inbreeding) could be elevated, following patterns seen in other species (Lieberman et al., 2011). Therefore, women in their periovulatory phase might initiate less contact with fathers, relative to mothers. To test this idea, Lieberman et al. (2011) used phone records over a month to assess contact and found evidence for this effect. Women called fathers less frequently and for fewer minutes during the periovulatory phase—and when fathers contacted them, the women ended the call sooner. A subsequent daily diary study found no evidence of reduced contact with male kin when women were conceptive (Holzleitner et al., 2018). But the study did not distinguish self- and kin-initiated contact, and only assessed contact with kin lasting at least an hour—which most women never experienced during the study—whereas the calls that Lieberman et al. (2011) tracked often lasted five minutes or less. A true replication study is needed.

THE POTENTIAL MODERATING IMPACT OF RELATIONSHIP QUALITIES ON HORMONAL EFFECTS

In multiple sections, we have illustrated the wisdom of estrous sexual choices by highlighting the potential importance of women's relationship status and

qualities on the fitness benefits of conception. Unpartnered women may not benefit from conceiving during the current cycle. Similarly, women partnered with men whose qualities they question or whose commitment is uncertain may benefit from avoiding conception in the current cycle. The dual sexuality framework begs for examination of how relationship qualities moderate women's sexual interests. Yet few studies to date address these moderation effects.

The Evolution of Human Pair-Bonding

Earlier, we noted that Thornhill and Gangestad's (2008) discussion of estrous preferences relied heavily on a phylogenetic perspective. They argued that, in mammalian species without extended sexuality, estrous females discriminate between mates. Especially in species in which males do not care for offspring (which are the vast majority of mammalian species), females benefit from choosing mates for their genetic qualities (though, in multimale/multifemale groups, male status can confer direct benefits even in the absence of overt male care; e.g., Alberts & Fitzpatrick, 2012). In many species with extended sexuality, the estrous phase may be characterized by these preferences as well.

The extent to which pair-bonding and paternal care evolved as central features of human mating and parental investment systems has been debated. Some have argued that humans have evolved "cooperative breeding" arrangements, through which alloparents (including kin) play crucial support roles (Hrdy, 2009); paternal care, though present, has not been the crucial nonmaternal source of care (e.g., Sear & Mace, 2008). By contrast, others have argued that paternal provisioning is a core element of a broader "human adaptive complex" (e.g., Kaplan et al., 2000) and a key predictor of women's total fertility rate (e.g., Marlowe, 2001; Winking, 2006). Some researchers have argued that romantic relationships evidence "special design" for human pair-bonding (e.g., universality of romantic love and attachments akin to those between parents and children; Fletcher et al., 2015; Pillsworth & Haselton, 2006b). Although polygyny is present in many societies, the most common mating arrangement even in polygynous societies is monogamy (e.g., Schacht & Kramer, 2019). The low extra-pair paternity rate in human societies examined to date is typically < 3% (versus a mean rate of ~10% in socially monogamous birds) and may be a telltale signature of substantial paternal contributions ancestrally (Schacht & Kramer, 2020; see also Thornhill & Gangestad, 2008). A notable exception is the extra-pair paternity rate (48 percent) in the Himba, a group of Namibian pastoralists; 70 percent of couples cared for at least one extra-pair child (Scelza et al., 2020; see also Beckerman & Valentine, 2002; Walker et al., 2010, on

widespread “partible paternity” in a substantial number of South American groups). The centrality of pair-bonding, male–female attachments, and paternal care in human reproductive systems ancestrally certainly could have varied—core in many socioecologies, but more peripheral in others (for more on cultural differences evoked by different ecologies acting on the same psychological mechanism, or “evoked culture,” see Gangestad et al., 2006; Tooby & Cosmides, 1989).

The Adaptive Workaround Hypothesis

Under the assumption that human pair-bonding has been highly important, Eastwick (2009) proposed the *adaptive workaround hypothesis.* This hypothesizes that women in strongly bonded relationships (as characterized by high levels of attachment phenomena, such as proximity maintenance) evolved adaptations to seek out sexual intimacy with their partners during the periovulatory phase. In two small studies, Eastwick and Finkel (2012) found provisional evidence for a predicted bond strength × phase interaction effect on women’s seeking out sexual intimacy with partners, with greater in-pair sexual interest during estrus by strongly bonded women.

The Dual Sexuality Framework as a Vehicle for Exploring Estrous Design Space

We have emphasized a selection constraint on estrous sexuality: It should have been shaped to guide women toward the wisest use of their relatively few lifetime opportunities to produce offspring. What constitutes wise decisions depends on ancestral selection contingencies not fully understood at this time, a point illustrated by the impacts of relationship qualities. The importance of pair-bonding and pair-bonding quality to offspring number and success has been debated. *If* pair-bonding has been crucial (or critical in at least some contexts), then we might expect women to experience increased sexual interest in partners during estrus—especially when partners are strongly attached. *If* pair-bonding has been less important, then we might expect women to be less exclusively interested in partners during estrus and for strength of attachment to weakly moderate cycle shifts in women’s sexual interests. The dual sexuality framework offers a principled basis through which to explore estrous design space (rather than entailing one specific prediction). For instance, the framework may permit principled understandings into how important pair-bond quality was for human reproduction ancestrally (e.g., Andrews et al., 2002; Williams, 1966). Studies examining how relationship qualities moderate women’s sexual interests may provide insight into estrous sexuality and the “special design” of estrous shifts.

Extended Sexuality

Extended sexuality evolved in humans because, ancestrally, nonconceptive sex yielded benefits. Logically, human extended sexuality was shaped to garner those benefits. What were these benefits? Just as with respect to estrous sexuality, the dual sexuality framework does not entail a single answer. It offers guiding principles for exploring the design space of extended sexuality. Below, we flesh out plausible contenders and discuss the possibility that ancestral benefits differed across contexts (e.g., for paired and non-paired women).

A CONTRASTING PERSPECTIVE: MOTIVATIONAL PRIORITIES

First, we return to a contrasting perspective, motivational priorities theory. As noted earlier, this perspective acknowledges social impacts on sexual desires. Whereas hormonal inputs regulate general sexual desire, social factors typically elicit target-specific interests. However, social factors exert additive effects on sexual desire, independent of hormonal inputs. If sexual activity functions in part to foster intimacy in a relationship, a woman's sexual desire for her partner would increase across all phases of the cycle.

In contrast, the dual sexuality framework views complete independence as unlikely. At times, females can garner benefits from nonconceptive sex precisely because it *is* nonconceptive. We discussed the example of paternity confusion in nonhuman primates earlier. Females copulate with males not preferred as sires when nonconceptive, leading male partners to "think" they may have sired an offspring. If females copulated with these males when conceptive, nonpreferred males *could* be sires. Extended sexuality evolved in these species precisely because it benefited females to have sex when conception is not possible and, as a result, reduce the likelihood that males harm offspring that they did not sire.

THE PAIR-BOND EXTENDED SEXUALITY HYPOTHESIS

We noted earlier that human extended sexuality may have been shaped to garner benefits in the context of pair-bonding. The pair-bond extended sexuality hypothesis argues further that human extended sexuality played a key role in the evolution of pair-bonding (Gangestad et al., 2015).

Humans likely evolved from a state of living in multimale/multifemale groups with strict dominance hierarchies and promiscuous mating (as in chimpanzees, from whom hominins diverged ~8 million years ago) to living in multimale/multifemale groups with pair-bonding and biparental care (e.g., Muller et al., 2017). But how did the transition occur? How did hominin males evolve to take an interest in offering care to offspring?

Once males sire an offspring, they can choose to care for that offspring, reenter a mating market and compete for new mating opportunities, or a combination of the two. Those most successful in a mating market (often dominant males) benefit most by choosing to compete for mating opportunities rather than by caring for offspring. Those least successful (often nondominant males) benefit most from choosing to care rather than to compete. In many species, however, males who would benefit by caring for offspring never have the chance to make that choice; they never sire offspring because (1) females benefit from choosing dominant males over submissive males who are likely to help care for offspring, and/or (2) dominant males successfully exclude non-dominant males from access to conceptive females. Hence, paternal assistance has not evolved in these species (which includes most mammalian species; Kokko & Jennions, 2008).

Mathematical models that simulate costs and benefits of different strategies find several conditions favoring the evolution of paternal care (Gavrilets, 2012). In multimale/multifemale groups starting from a state with no paternal care, first, females benefit from male care (typically through increased rates of offspring production), and therefore evolve to choose males interested in provisioning; second, females can evolve to be "faithful" to male caregivers they choose as partners, establishing a pair-bond with partners to produce offspring; third, and less intuitively, pair-bonding and paternal care can emerge when male competitive abilities and levels of dominance vary substantially. This last condition is crucial; when it is met, nondominant males benefit by provisioning offspring, thereby satisfying females' preferences and reinforcing their faithfulness. Under biologically realistic conditions, the evolutionary dynamics in these models lead to all but the most dominant males provisioning offspring. Female faithfulness evolves to be very substantial, though not perfect, even when most males provisioned. (In two different models differing in group size, rates of faithfulness—expressed as a share of offspring sired by provisioning males—evolved to be 0.85 and 0.70. This outcome implies that, in the models' stable state, males sometimes provision offspring that are not their own. This may seem maladaptive, but the alternative—reentering a competitive mating market—serves nondominant males even more poorly. As a result, a "dual mating strategy"—whereby females selectively mate with dominant males for genetic benefits but receive provisioning from non-dominant males—can evolve, though only when provisioning males sire most offspring.)[7]

These models assume that female preferences for males who provision will evolve, which implies that females can freely choose to mate with nondominant males likely to offer parental care. Despite female mate preferences, however,

dominant males may still monopolize sexual access to the females that are in estrus. (For a discussion of this phenomenon in chimpanzees, see Muller et al., 2011.) Dominant males can most effectively prevent nondominant males from mating with females in estrus when female conceptive status is readily discernable. Their ability to monopolize matings during estrus diminishes when female conceptive status is uncertain. Accordingly, Strassmann (1981) proposed that women evolved to suppress cues of estrus, thereby freeing their ability to choose nondominant males as partners.

If dominant males lack the ability to detect conceptive status, females' pair-bond partners may as well. Regular sex throughout a woman's cycle may enhance her romantic partner's confidence that offspring are his own, as he cannot reliably discern when she is in estrus. As a result, the extension of women's sexual interests into nonconceptive phases of the cycle may have been favored by selection to enhance male partner investment in offspring (Strassmann, 1981). This perspective views human extended sexuality as functioning, in part, to solidify pair-bonds and to enhance the paternity confidence of romantic partners (see also Alexander & Noonan, 1979). Selection may have shaped extended sexuality in ways that garner these benefits (Thornhill & Gangestad, 2008).

STRATEGIC ELEMENTS OF EXTENDED SEXUALITY

Extended sexuality may have evolved to become sensitive to relationship features that strategically call for bolstering investment and bonding. Consistent with this proposal, in one study following fifty women over one cycle, women initiated more sex with partners during extended sexuality when they were invested in their relationships, but they perceived that their partners' investment lagged behind their own (Grebe et al., 2013). Highly invested women perceiving a lack of male partner investment may engage in behaviors—through extended sexuality—that function to foster paternity assurance and, consequently, bolster her partner's interest in the relationship. As the authors explicitly acknowledged, this study was merely "a preliminary step toward understanding women's extended sexuality"; as the small study was "itself not definitive," its "most important contribution … is to illustrate the theoretical importance and empirical fruitfulness of examining extended sexuality, in contrast to the recent focus on women's estrus" (p. 2109). Relatedly, an earlier study not designed explicitly to test ideas about extended sexuality found that women's interest in sex-for-intimacy increased during extended sexuality, consistent with a bonding function (Sheldon et al., 2006). These ideas triggered research examining interactions between relationship features and use of hormonal birth control with more

estrogenic (estrus-like), compared to progestogenic (extended-sexuality-like), formulations. Results provided supportive evidence for pair-bonding functions of women's sexuality when progesterone levels are high (Grøntvedt et al., 2017). Still, definitive evaluations of these and related ideas about extended sexuality have yet to appear.

Estrous sexuality, too, could be sensitive to relationship features. For example, the adaptive workaround hypothesis predicts that estrous women will be especially attracted to partners, relative to extra-pair men, when the pair-bond is strong—when both female and male partners are highly invested in their relationships (Durante et al., 2016). And during extended sexuality, according to the pair-bond extended sexuality hypothesis, women will be especially attracted to partners relative to extra-pair men when there is a discrepancy between female and male investment. Therefore, although relationship features may provide inputs into both estrous and extended sexuality, effects will differ because the functions of estrous and extended sexuality differ.

Estrous and extended sexuality may also be sensitive to different facets of relationship functioning. The adaptive workaround hypothesis predicts that bond strength will moderate associations between conceptive status and women's sexual interests. The earlier work on extended sexuality did not explicitly distinguish facets of relationship involvement to which extended sexuality may be sensitive (Grebe et al., 2013). If extended sexuality functions to solidify bonds not fully established, then intense romantic interests may importantly predict sexual interests during extended sexuality. If extended sexuality functions to maintain bonds that are already well established, then bond strength may importantly predict these sexual interests. These possibilities are not mutually exclusive.

ALTERNATIVE FUNCTIONS OF EXTENDED SEXUALITY

The pair-bond extended sexuality hypothesis proposes that women's extended sexuality evolved in the context of pair-bonding. Yet once extended sexuality evolved in humans, and women possessed the ability and willingness to engage in nonconceptive sex, even those not currently involved in a romantic relationship could gain benefits. The benefits single women could garner from nonconceptive sex were likely very distinct from the benefits partnered women could seek. One possibility is that extended sexuality in nonpartnered women evolved to assess potential partners' qualities and willingness to invest in a future relationship. Having sex during estrus entails the potential cost of untimely reproduction. In theory, single women could use extended sexuality to assess male qualities (or, alternatively, acquire direct benefits) without

committing to a possible pregnancy.

The dual sexuality framework offers broad guiding principles for exploring the design space of extended sexuality. Above, we focused on ways that extended sexuality may regulate investment by male relationship partners. Alternative functions can also be explored (see, e.g., Geary et al., 2011, for a perspective on female–female competition).

MALE COUNTERADAPTATIONS

The argument that female extended sexuality evolved in part to garner benefits from males relies on the assumption that males cannot perfectly discern female conceptive status. If they could, then they would be aware of a woman who might only mate with them on her nonconceptive days, and they could theoretically adjust their investment in her and her offspring accordingly. In theory, women have evolved to conceal cues of ovulation to prevent this. However, males who could better discern female conceptive status would have had higher fitness. Co-evolution of the sexes—with females evolving to better conceal their conceptive status and males evolving to better detect or estimate it—could have reasonably occurred. Based on the theoretical arguments and empirical patterns of female sexuality in humans and nonhuman primates described above, we surmise that, at least in humans, cues of female conceptive status are relatively weak; males are unable to reliably discern female conceptive status; and males may possess adaptations that crudely estimate female conceptive status, given sufficient information (e.g., being in close proximity to a romantic partner for extended duration), but these estimations are error-prone. And because of the relatively low costs of sex to men and high potential benefits of reproduction, men may be motivated to have sex throughout most of a woman's cycle. From an error management perspective (Haselton & Buss, 2000; Haselton & Nettle, 2006), a non-zero probability of potentially siring an offspring can effectively retain male sexual interest during extended sexuality. Men may be interested in sex across his partner's cycle but still have some guess of when conception probability is likely higher during one point of the cycle, compared to another. But because conception probability across the cycle is graded, sex on days outside of peak fecundity can still lead to conception. Men are probably unable to reliably discern whether their chance of siring an offspring is non-zero.

Nevertheless, men should have evolved to reduce the costs of potential deception by female partners. Data from several studies find that male partners relatively low in sexual attractiveness are more likely to exhibit mate-guarding behaviors during their partner's conceptive phase (Gangestad & Dinh, 2021;

Gangestad et al., 2002; 2014; Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006a). Men may also be selected to adjust their level of investment, conditional on the probability of paternity. However, "deception" by female partners need not imply extra-pair copulations. Rather, extended sexuality may offer women the benefits of delaying reproduction while assessing male willingness to invest. In this instance, the costs to the male of being "deceived" may be low, and the costs of withdrawing investment may be very high (e.g., losing a reproductive partner).

Women's estrous and extended sexuality likely have overlapping functions, one of which may be to influence male investment. For instance, women highly invested in their romantic relationship may maintain high levels of sexual interest in their partner across estrus and extended sexuality, as regular sexual activity across the cycle may function to encourage, or avoid loss of, valued partner investment (Grebe et al., 2013). This may possibly explain why partner sexual attractiveness generally does not appear to moderate ovulatory shifts in women's in-pair sexual interests (e.g., Arslan et al., 2021; Gangestad & Dinh, 2021). Avoiding sexual activity with an investing partner during the periovulatory phase could threaten loss of partner investment.

Evaluating the Evidence for Hormonal Influences on Libido

We have contrasted the dual sexuality framework with an alternative view, motivational priorities theory. In the latter perspective, hormonal influences on sexual interests are simple: estradiol boosts and progesterone suppresses libido. Theoretical reasons lead us to be skeptical that selection would yield this outcome, and to question whether libido meaningfully explains women's sexual interests. Nonetheless, some scholars have argued that findings offer broad support for this theory (e.g., Jones et al., 2018a, 2018b; Roney, this volume; Stern & Penke, this volume). In fact, the empirical support for motivational priorities theory is not compelling. Supportive evidence may seem consistent with the theory's claims but does not rule out alternatives. Moreover, other evidence is inconsistent with the theory.

HORMONAL INFLUENCES ON MEASURES OF SEXUAL INTEREST

In studies claimed to support motivational priorities theory, women's estradiol levels positively and/or progesterone levels negatively predicted their ratings of their current level of "general" sexual desire or "current sex drive" (e.g., "How much do you desire sexual contact today?"; Roney & Simmons, 2013; Jones et al., 2018b; see also Stern et al., 2021). From these data, Jones et al. (2018b)

conclude, “hormonal changes contribute to changes in women’s general sexual desire” (p. 153). Yet this inference goes well beyond the data. Women were asked whether they desired sexual contact, but their desires could have been very specific to particular targets (such as a current partner or “crush”). Ovarian hormones may affect, on average, the potential for sexual interests, but in no way does that imply that interests are “general.”

Proponents of motivational priorities theory also point to positive associations between conceptive status and both in-pair and extra-pair sexual interests (e.g., Arslan et al., 2021). In fact, this pattern has not always been found. A study of more than twenty thousand normally cycling women from developing countries showed no phase differences in rates of copulation with primary partners, aside from a drop at menses (Brewis & Meyer, 2005). In small samples, two studies found greater effects of conceptive status on extra-pair than in-pair attraction (Gangestad et al., 2002, 2005; see also Shirazi et al., 2019b; cf. Shirazi et al., 2019a). Two other studies found that progesterone levels *positively* predicted and/or estradiol levels *negatively* predicted women’s in-pair attraction (Grebe et al, 2016; Righetti et al., 2020).

These variations notwithstanding, evidence may suggest *average* phase effects on in-pair and extra-pair sexual interests running in the same direction. Once again, however, one cannot infer that because average effects on in-pair and extra-pair interests run in the same direction, shared effects on libido, rather than much targeted interests, are responsible. If libido affects both in-pair and extra-pair interests, one might expect in-pair and extra-pair interests to positively covary (in the way that a shared factor of “general” intelligence generates a positive manifold of correlations between separate measures of cognitive performance). Yet women’s in-pair and extra-pair interests covary *negatively* (Arslan et al., 2021; Dinh et al., 2017 (unpublished analyses)). The group-level pattern of average effects—greater mean in-pair interest and extra-pair interest when women are conceptive—need not apply to individuals. Average effects may reflect moderation—the result of some individuals driving one set of effects, while others driving another set of effects—often leading to overall weak effects. This possibility may characterize the small but statistically detectable effects found in studies. For example, a massive study of 3.3 million women in 109 countries found that women were only about 3% more likely to have sex during the mid-to-late follicular phase (days 8 to 14 of their cycles), compared to the midluteal phase (reverse count days -10 to -4) (Pierson et al., 2021).

MODERATOR EFFECTS AND THE LIBIDO EXPLANATION

The main effects predicted by motivational priorities theory may emerge even

in the presence of complicating moderator effects—though, in such cases, they should depend on the distribution of the moderating factors in the sample examined. The fact that studies have yielded varying patterns may well reflect moderator effects. Differences in how samples are recruited can affect the estimated averages of populations from which they are drawn. If those populations vary on important moderators (e.g., relationship qualities), differences between samples can incidentally generate variable patterns across studies. Atypical patterns of main effects (e.g., Righetti et al., 2020) should not be dismissed as meaningless.

The dual sexuality framework argues that hormonal influences are more complicated. Hormonal effects on both in-pair and extra-pair sexual interests are likely to depend on specific conditions, including ones we have discussed (e.g., partner attractiveness and relationship qualities). Moderator effects may be stronger tests of specific proposals within the dual sexuality framework. They are also pertinent to evaluating motivational priorities theory, as the perspective cannot explain most moderator effects.

As we reviewed earlier, evidence to date for the partner attractiveness moderator effect is strong. Multiple studies, including recent replication studies, have yielded findings consistent with partner sexual attractiveness × conceptive status interaction effects on extra-pair sexual interests. Motivational priorities theory does not explain these effects. Evidence for moderator effects of relationship qualities on the association between hormone levels and sexual interest is currently provisional. Future assessments of these associations will be pertinent to evaluating both the dual sexuality framework and motivational priorities theory.

THE PURPORTED TRADE-OFF BETWEEN SEXUAL DESIRE AND APPETITE

Over three decades ago, research found that women consume more food during the mid-to-late luteal phase than during the periovulatory phase (e.g., Lissner et al., 1988). After reviewing this literature, Fessler (2003) documented similar changes in a variety of nonhuman primates and mammals and presented evidence that, mechanistically, hormones regulate thresholds of satiety. He also proposed a functional explanation: females suppress appetite when conceptive because foraging, instigated by hunger, competes for time and energy allocation with mating effort. In Fessler's view, this mating effort was typically dedicated to searching for mating opportunities outside of those immediately available (such as, in humans, extra-pair opportunities).

Subsequently, Roney and Simmons (2017) proposed a trade-off between appetite/foraging and general sexual desire, rather than mate search specifically.

They hence incorporated findings on appetite shifts into the motivational priorities perspective. They also found, as an empirical signature of trade-offs, a negative within-woman association between food intake and sexual desire. Their sample contained only nine partnered women and could offer no definitive tests of alternative conceptualizations, such as Fessler's account.

In the largest study of cycle shifts in women's food intake to date, which tracked 259 women over one to two cycles, no phase differences in overall energy consumption were detected (though effects were directionally consistent with past reports; Gorczyca et al., 2016). Examination of shifts in consumption of specific macro- and micronutrients revealed that women ate more animal protein during the luteal phase. Despite finding no phase differences in overall carbohydrate consumption, the study detected increases in cravings for chocolates, sweets, and salty foods during the late luteal phase. How hormones affect patterns of food intake is yet to be fully understood.

Nonetheless, there is clear evidence that appetite shifts in some way across the cycle. These effects may inform an understanding of estrous and extended sexualities but evidence currently available does not strongly favor the specific explanation proposed by motivational theory, as some have implied (e.g., Stern & Penke, this volume). Fessler's (2003) alternative proposal fits comfortably within the dual sexuality framework, and it has not been ruled out (see Thornhill & Gangestad, 2008, for other alternative models not yet fully explored).

THE COMPARATIVE LITERATURE ON SEXUAL DESIRE

Roney (2018) has argued that there exists a "general mammalian pattern of positive effects of estradiol and negative effects of progesterone on measures of female sexual motivation" (p. 245), which has been conserved in humans. Most spontaneously ovulating mammalian females are sexually active only during estrus; they do not possess extended sexuality. Nonhuman primates frequently possess extended sexuality, but their sexual interests do not uniformly follow the "general mammalian pattern" Roney assumes to exist. For instance, in humans' closest extant relative, chimpanzees, females initiate copulation more on days that fall outside the periovulatory phase than inside it (especially with males not preferred as sires; Stumpf & Boesch, 2005). Yet, like humans, their estradiol levels peak during the periovulatory phase, and their progesterone levels do not markedly rise until the luteal phase (Emery & Whitten, 2003)—which highlights how female chimpanzee sexual motivation does not follow the patterns of hormonal inputs posited by Roney (2018). Moreover, in some other nonhuman primates, females actively solicit sex with submissive males only after ovulation, when estradiol levels have fallen and progesterone levels risen (Dixson, 2012).

Female sexuality in nonhuman primates cannot be understood in terms of a simple two-input hormonal code regulating "general" sexual desire. Far from supporting a "general mammalian pattern" that has been conserved in humans, the comparative literature supports the alternative view that, in species with extended sexuality, selection has shaped female sexual interests to be strategically textured across conceptive and nonconceptive days.

Dual Sexuality as a Scientific Framework: Reflections on Theory Development and Testing

Dual sexuality is a theoretical framework. It asserts that women's estrous sexuality and extended sexuality evolved to garner different benefits, in part, and hence evolved to regulate sexual interests in response to stimuli and conditions in nonidentical ways. While explanation within the framework is constrained (e.g., it must recognize that estrous sex is conceptive), the framework does not, a priori, fully commit to any specific understanding of the sexualities. Evidence weighing against specific proposals may prompt alternative proposals within the framework and, indeed, potentially a supported variant that *is* specific. Because it may seem that theory modifications could persist *ad infinitum*, however, some scholars may be concerned that the framework is not falsifiable (Popper, 1959; see Stern et al., 2019). In response, we explain how the framework fits within a Lakatosian perspective on "research programs" and propose that use of similar frameworks within the evolutionary sciences is scientifically profitable.

ARE OPEN THEORIES FALSIFIABLE?

Popper (1959) noted that whereas scientific theories cannot be confirmed, they can be falsified. If theory T implies observation O, then, *modus tollens:* if ~O, then ~T. Failure to falsify a theory does not mean it is true (affirming the antecedent is a logical fallacy). But theories surviving falsification (e.g., by correctly predicting a surprising observation) are worthy of further consideration. As Popper recognized and Lakatos (1970) emphasized, tests of theory always rely on auxiliary assumptions (e.g., about the validity of methods). Moreover, theories are not single statements but, rather, consist of multiple assertions (e.g., T = T_1, T_2, T_3 …, T_k, where T is the "theory" and T_1 to T_k, are *k* assertions within the theory). When a theory fails to correctly predict an observation, the "theory" may be falsified (if auxiliary assumptions are sound) but, logically, no individual theoretical assertion is definitively falsified; ~O → ~ (T_1 and/*or* T_2 … and/*or* T_k).

When empirical anomalies arise, scientists often modify a theory, altering or

adding at least one theoretical assertion. Some assertions are more "core" to a theory, others more "peripheral." Scientists often preferentially modify peripheral assertions while retaining a "hard core," and do so iteratively in the face of subsequent anomalies. In this way, scientists may falsify (narrower) theories but avoid falsification of core assertions within a (broader) theoretical approach (Lakatos, 1970).

Lakatos (1970) referred to iterative rounds of modification and test directed by a theoretical approach as a "research program." Research programs can be "progressive" or "degenerative": progressive when empirical content explained by the theory is expanded, as peripheral modifications generate new predictions that survive tests; degenerative when modifications are nongenerative or fail to receive support. When research programs are abandoned, it is not typically when core assertions are falsified. Rather, an approach withers when a rival research program, one that invokes alternative core assertions, is more progressive.

The dual sexuality framework can be thought of as a research program in this sense. Its hard core asserts that estrous sexuality and extended sexuality evolved to be distinct, in some ways, and imposes constraints on the kinds of benefits that shaped each sexuality. Specific theories within the framework (e.g., the ovulatory shift hypothesis and the dual mating hypothesis) flesh out peripheral assertions. These peripheral assertions, however, are explicitly flexible, such that estrous sexuality and extended sexuality are intentionally open concepts (e.g., Meehl, 1986). The program may lead to specific theoretical formulations that survive falsification—but, if it fails to do so, it will wither.

OPEN FRAMEWORKS WITHIN EVOLUTIONARY PSYCHOLOGY

Inclusive fitness theory (Hamilton, 1964), the modern conception of Darwin's theory of natural selection, constrains ideas about plausible designs shaped by selection (e.g., that we tend to favor kin over nonkin) but does not predict exactly how selection will have shaped a given species. Rather, predictions depend on details of past selective environments. In making predictions about human behavior, evolutionary psychologists implicitly or explicitly make assumptions about past selection. But if predictions are wrong, we do not think that the theory of natural selection is flawed; instead, failure is typically blamed on faulty assumptions about past selective environments. A revised set of assumptions may improve predictions.

The dual sexuality framework explicitly embodies uncertainties of past selective environments. How important was paternal investment to female fertility rates? What was the fitness impact of genetic benefits relative to increments in paternal investment? To what extent were male levels of

investment sensitive to levels of paternity certainty? Assuming cues of conceptive status were suppressed but not eliminated in ancestral women, how much information did residual cues carry? Answers to these questions, and many more, are unknown—yet precise predictions about how estrous and extended sexuality differ, and to what features and conditions they are sensitive to, may depend on answers. Specific "subresearch programs" that fall within the framework provisionally assume answers. Empirical anomalies prompt modifications. If the resulting research program is progressive, the initial "openness" of our understanding of estrous and extended sexuality will "fill in" (Meehl, 1986).

The dual sexuality open framework resembles other efforts in the field that are progressive theory-revising, -building, and -testing enterprises (such as the active debates concerning human life history theory (e.g., Frankenhuis & Nettle, 2020).

The Dual Sexuality Framework and Future Research

Women's sexual activity across variable hormonal conditions is extraordinary; how selection shaped this feature may be extraordinary too. Nonconceptive sex evolved to garner benefits distinct from conception. Accordingly, the modes of sexuality operating during estrus and extended sexuality likely differ as well. Estrous sexuality should have been shaped to yield wise reproductive decisions ancestrally. Extended sexuality may have been shaped to yield other benefits, precisely because sex during extended sexuality is nonconceptive. The dual sexuality framework gives rise to a variety of hypotheses about how the two sexualities were shaped, in complementary and competing ways. Some lines of work (e.g., on the ovulatory shift hypothesis and moderation effects of partner attractiveness) have received much attention, yielding a complicated literature yet to be fully understood. Others have received very little attention (e.g., on fertility-regulation adaptations, and moderation effects of relationship qualities); they represent potentially fruitful directions for future research. Importantly, research inspired by the dual sexuality framework may lead to a better understanding of hormonal influences on human sexuality and, more generally, the special design of estrous and extended sexuality. This line of research could offer profound and fundamental insights into human mating and reproduction.

Notes

1. In many mammalian species (e.g., rabbits, raccoons, and domestic cats), ovulation is induced by copulation, at least in part. In many other species, including all primates but also substantial portions of other mammalian orders, females spontaneously ovulate during reproductive cycles, with or without copulation. Spontaneous ovulation may have evolved to facilitate female sire choice (e.g., Pavliček & Wagner, 2016).
2. The term "estrus" (and its adjectival form, estrous) was originally applied to a circumscribed sexual phase. However, functionally, estrous sexuality should regulate female conceptive sex, whether or not females possess extended sexuality. We retain the term "estrus" here to refer to conceptive-phase sexuality and *extended sexuality* to refer to sexuality outside the conceptive phase (Thornhill & Gangestad, 2008).
3. For additional discussion of issues, see Gangestad et al. (2019b), Stern et al. (2019), and Del Giudice and Gangestad (2021).
4. This finding was mistakenly claimed to be a failure to replicate (see also Jones et al., 2018b) because the simple effect of phase when partner attractiveness was centered at 1 SD below the mean fell short of statistical significance, $p = 0.12$. Sample size was just forty women. When an interaction effect is significant, and mean differences all fall in expected directions, asserting a "failure to replicate" because one simple effect *p*-value was 0.12, with small sample size, is simply not justified (e.g., Amrhein et al., 2019). Despite small sample size, the interaction effect in question replicated.
5. Even before errors were corrected, Arslan et al.'s analyses yielded multiple $p < 0.01$, but they did not report these *p*-values in text. See Gangestad and Dinh (2021).
6. Though evidence is mixed, support for the hypothesis that partner attractiveness moderates ovulatory shifts in attraction to the partner is generally weak (e.g., Arslan et al., 2021; Gangestad & Dinh, 2021). One possibility is that avoiding sexual activity with an investing partner during the periovulatory phase could threaten loss of partner investment.
7. Naturally, these modeling results do not imply that "dual mating" is the sole or even primary reason for infidelity (e.g., Buss et al., 2017). In addition, we do not suggest here that modeling implies an extra-pair paternity rate of 15 to 30 percent. The models here do not account for the possibility that male mate guarding or detection of nonpaternity (e.g., through phenotype matching) may further suppress rates of infidelity.

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CHAPTER
31

Ovulatory Cycle Effects and Hormonal Influences on Women's Mating Psychology

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Abstract

Do hormones affect women's mating psychology? In which way? Why? In this chapter, we address these questions and summarize the current evidence on associations between women's ovulatory cycle, hormonal changes, and their mating psychology. We focus on potential changes in sexual motivation, mate preferences, and attraction to potential mates. We further evaluate potential changes in cues to fertility, whether they are detectable by others and whether these changes lead to corresponding affective and behavioral changes in romantic partners. We also discuss the potential implications of research on hormonal contraception on mating and point out reasons why some findings might not replicate.

Key Words: ovulatory cycle, steroid hormones, mate preferences, sexual desire, cues to fertility

Human Estrus

Most mammalian females experience reproductive cycles (also known as ovulatory cycles), varying in typical length from species to species. In human females, alongside some other primates like chimpanzees and many simians, these cycles are marked by shedding and vaginal ejection of the uterine lining as menstrual bleedings, which is why these cycles are called menstrual cycles in these species. Menstrual cycles are usually characterized by two different phases: the follicular phase begins with menstrual bleeding and ends with ovulation, which then introduces the start of the second phase, the luteal phase.

Conception is only possible in the fertile period of each cycle, in human females up to six days, usually the day of ovulation and the five days prior. The different cycle phases are characterized by substantial hormonal changes, especially in the reproductive hormones estradiol and progesterone: Whereas estradiol levels are usually higher in the follicular phase and peak around the day of ovulation (with a second, smaller peak midluteal), progesterone levels are lower in the follicular phase and rise in the luteal phase, peaking around midluteal.

Females of many nonhuman mammals only actively engage in sex (proceptivity) and accept male advances for sex (receptivity) when conception is possible (i.e., when they are fertile), and signal their fertility by changes in appearance and behavior toward males. This phenomenon of mammalian reproductive biology is widely known as estrus or heat, and it is defined as a "relatively brief period of proceptivity, receptivity, and attractivity in female mammals that usually, but not invariably, coincides with their brief period of fertility" (Symons, 1979, p. 97). The question whether human females also experience estrus has long been discussed. Women experience extended sexuality, which means that they do not only engage in sexual behavior when fertile but also at other times across the cycle or postmenopausal. Further, women do not show obvious changes in appearance or behaviors across their cycle. These facts led to the assumption that (classically defined) estrus was lost in human females, possibly due to the evolution of pair-bonding, to ensure paternal investment in their offspring and reduce infanticide (Alexander & Noonan, 1979; Rooker & Gavrilets, 2020; Symons, 1979). However, the lost estrus claim has been challenged by findings suggesting that there are, indeed, psychological and behavioral changes across the ovulatory cycle. Although these changes seem not to be as obvious as estrus changes in some nonhuman mammals, they suggest that estrus was not lost in humans, despite the evolution of extended sexuality (Thornhill & Gangestad, 2008). Nevertheless, women do not show classically defined estrus in that they are only sexually active during a restricted fertile period. Changes in appearance or women's mating psychology across the cycle, in line with human female estrus, might be rather subtle and probably predominantly characterized by changes in the nature of women's sexual interests.

Ovulatory Cycle Effects on Women's Mating Psychology

In which way do women's sexual interests change across the cycle? There are different hypotheses about potential changes in line with human estrus and multiple studies investigated these. Here, we review the most prominent ones

and discuss the current state of evidence.

The Good Genes Ovulatory Shift Hypothesis

Probably the most prominent hypothesis in this research area is the *good genes ovulatory shift hypothesis* (GGOSH). It predicts that women's mate preferences, thus with whom they aim to mate, change across the cycle to increase genetic benefits for their offspring. More precisely, this hypothesis makes three directly testable predictions (Gangestad et al., 2005; Gildersleeve et al., 2014): First, when fertile, women should be more sexually attracted to male characteristics that indicate genetic quality, compared to their low-fertility days. Second, cycle shifts in women's mate preferences for genetic quality indicators should be absent or only weakly present when evaluating men for long-term relationships (i.e., not only their sexual attractiveness). Third, when fertile, women should not be more sexually attracted to men's characteristics that reflect a higher suitability as a long-term partner. Pillsworth and Haselton (2006) expanded these ideas and hypothesized that women may have evolved a dual mating strategy in which they secure investment through their (long-term) bonding partner, while obtaining good genes for their offspring through extra-pair copulations with other men when fertile. These extra-pair copulations when fertile might especially happen when their partner lacks in displaying indicators of genetic quality. But how can women know which man possesses good genes? Indicators of genetic quality are hypothesized to be characteristics that signal superior immune functioning or are costly to produce and maintain, as only highly fit individuals in good phenotypic condition can afford to invest resources in these traits. Indirectly, such characteristics should thus be indicative of low mutation load, compatible genes, and genes well fitted to the current environment (i.e., "good genes") (Gangestad et al., 2015, Gildersleeve et al., 2014). Characteristics that have been assumed to reflect good genes in men were higher testosterone levels, dominant behavior, physical attractiveness, symmetry, and masculinity. Importantly, though, some purported indicators of good genes are controversial, because reported findings challenge the hypothesis that they actually signal heritable fitness benefits and immunocompetence (e.g., Nowak et al., 2018; Scott et al, 2012, 2014).

There are a large number of studies reporting supportive evidence for the GGOSH. When fertile, women report to prefer short-term sexual relationships with men who have more masculine or symmetrical faces (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000), masculine or muscular bodies (Little et al., 2007), masculine (deeper) voices (Feinberg et al., 2006; Puts, 2005, 2006),

masculine scent (Gangestad & Thornhill, 1998; Havlíček et al., 2005), and men who show more dominant behaviors (Gangestad et al., 2004, 2007). Further, changes in the target of women's sexual desire have been reported. In a study by Gangestad et al. (2002), women reported more sexual fantasies with men other than their primary partners when fertile. Women's increase in extra-pair desire in the fertile phase seems to be especially pronounced when they perceive their partner less sexually attractive, interpreted as a lack of genetic quality (Haselton & Gangestad, 2006), and has been linked to higher estradiol levels (Grebe et al., 2016). In contrast, sexual desire for women's primary partner might be higher when progesterone levels are higher, which usually marks the nonfertile, luteal phase (Grebe et al., 2016). To capture the idea that women's conceptive versus nonconceptive sexual interests may not be identical, Thornhill and Gangestad (2008) proposed the concept of *dual sexuality*. While sexual behavior outside the fertile phase may have evolved for pair-bonding purposes to secure long-term investment and protection from primary partners, the most obvious benefit for sexual behavior within the fertile phase is conception, which might be most adaptive to secure from different, genetically fitter partners. Hence, sexual interests should vary across the cycle accordingly.

While the evidence for the GGOSH has long been perceived as being convincing, doubts arose around 2014, when two meta-analyses focusing on shifting mate preferences across the cycle were published and came to strikingly divergent conclusions about the existence of these effects (Gildersleeve et al., 2014; Wood et al., 2014). As a consequence, a number of different researchers collected new data to investigate the robustness of changes in women's mate preferences and sexual desire across the cycle. In most of these newer studies, previously reported evidence in line with the GGOSH did not replicate. More precisely, recent studies based on more extensive data and more rigorous methods than earlier ones reported fertile-phase increases in both extra-pair and in-pair sexual desire (Arslan et al., 2021), and positive association of estradiol and negative of progesterone with general sexual desire (Jones et al., 2018a; Roney & Simmons, 2016) rather than specific shifts in extra-pair desire. Further, no compelling evidence was found for hormonal associations or ovulatory cycle shifts in mate preferences for men‘s faces (Dixson et al., 2018; Jones et al., 2018b; Marcinkowska et al., 2018a), bodies (Jünger et al., 2018a; Marcinkowska et al., 2018a; van Stein et al., 2019), voices (Jünger et al., 2018b), and behaviors (Stern et al., 2020). In contrast, other recent studies reported some evidence in line with the GGOSH, as changes in estradiol and progesterone were not associated with general sexual desire but with changes in short-term mating orientation (Shirazi et al., 2019) or extra-pair desire when fertile (Grebe et al.,

2016). Further, a reanalysis of Jünger et al. (2018a, a study reporting null results) argued to find evidence for changes in mate preferences for men's bodies (Gangestad et al., 2019). However, the latter has been criticized because of analytical decisions and challenged again by a multiverse analysis showing no robust evidence for cycle shifts in preferences for men's bodies with the same data (Higham, 2019; Jones et al., 2019b; Roney, 2019; Stern et al., 2019). Meanwhile, an even larger study did not replicate evidence in favor of the GGOSH, as reported in the reanalysis (Stern et al., 2021). Overall, recent nonreplications call into question all different lines of previous evidence in supportive of the GGOSH and make it unlikely that previously reported effects are robust (Jones et al., 2019a) or, at least, challenge the GGOSH as it is currently formulated (Stern et al., 2021). The controversy seems to be ongoing, but on balance very convincing new evidence in support of the GGOSH would be necessary to still regard it a plausible explanation of cycle shifts in women's mating psychology. Meanwhile alternative hypotheses have been developed.

Motivational Priority Shifts

Based on life history theory, the *motivational priority shifts hypothesis* (MPSH; Roney, 2018, for more details, see also Roney, this volume) suggests that women's motivations might change across the cycle to reflect varying costs and benefits of behaviors across cycle phases. When women can conceive, their mating motivation (e.g., general sexual interest) has a greater priority because the probability of conception provides a fitness benefit that outweighs potential costs of sex. Other motivations (e.g., somatic motivation to forage and eat) receive less priority in the fertile phase but increase during cycle phases when women cannot conceive (e.g., the luteal phase). Motivational priority shifts should mainly be regulated by fluctuating ovarian hormones, especially estradiol and progesterone. Other, nonhormonal effects (e.g., relationship status) might also have effects on shifting motivations, potentially independent of hormonal effects. A number of recent studies provided evidence in line with this hypothesis: In a diary study with naturally cycling women, Roney and Simmons (2017) collected daily hormone samples and self-reported food intake (how much participants ate during each meal) across one cycle. In line with lower motivations to forage and eat when fertile, participants reported a drop in food intake on the days approaching ovulation. Shifts in food intake were positively predicted by progesterone and negatively by estradiol levels. Further, for the same sample of participants, Roney and Simmons (2013, 2016) reported an increase in general sexual desire when fertile, with positive effects of estradiol

and negative of progesterone. More evidence for an increase in either general sexual desire or both in-pair and extra-pair desire when fertile (Arslan et al., 2021; Jones et al., 2018a) further support this hypothesis. While not necessarily assuming shifting mate preferences across the cycle, shifts in mate attraction, with all men being evaluated as a little more attractive when fertile, have been interpreted as being in line with the MPSH (Jünger et al., 2018a, 2018b; Stern et al., 2020). However, in a newer study Stern et al. (2021) replicate shifts in mate attraction but also report them to be very weak. Moreover, previous studies reporting mate preference shifts, or shifts specifically in extra-pair sexual desire, may not be in line with the MPSH.

Between-Cycle or Between-Women Effects

Rather than shifting within cycles, women's mate preferences or attraction might either shift between cycles within the same woman. Cycles with higher estradiol levels might be on average "more fertile" with a higher probability of conception (Roney & Simmons, 2013). Thus, women might experience shifts in preferences or attraction in cycles with higher estradiol levels. This hypothesis would predict preference or attraction shifts associated with specifically estradiol levels across cycles (Lukaszewski & Roney, 2009). However, evidence for links between estradiol and shifts in mate preferences is mixed, as reviewed by Roney (this volume), and in fact most studies did not directly assess hormone levels.

Rather than between cycles within the same woman, mate preferences and attraction, as well as sexual desire, might vary between women, potentially due to interindividual differences in hormone levels. In line with this assumption, the perceptual spandrel hypothesis has been proposed. This hypothesis states that variability in women's attractiveness and their mate preferences might not have been developed as an adaptation but rather are a by-product of between-women differences in hormone levels (Havlíček et al., 2015). Women with higher estradiol levels should possess a higher mate value, because they are generally evaluated as more attractive than women with lower estradiol levels. Thus, due to mate value-contingent preferences (Penke et al., 2007), and as more attractive women express higher standards for hypothesized indicators of good genes (Buss & Shackelford, 2008), they should also prefer more attractive men as partners. Whereas evidence for this hypothesis is scarce, some studies suggest that, indeed, changes in women's mating psychology may occur due to between-women, not within-women, hormonal effects. Rather than estradiol, progesterone levels, interacting with women's relationship status, were reported to predict between-women differences in mate preferences for masculine faces

(DeBruine et al., 2019; Marcinkowska et al., 2018b). This interaction effect was not replicated for preferences of men's bodies (Stern et al., 2021). Independent of differences in hormone levels, a large study with 2,160 twins and their siblings suggests that different mate preferences for masculine faces are rather due to genetic variation than to contextual factors, such as fluctuations across the cycle, providing more evidence for between-subjects effects (Zietsch et al., 2015).

Other Hormonal Influences on Women's Mating Psychology

Other hormones beyond estradiol and progesterone, especially testosterone and cortisol, have been considered to influence women's mating psychology, particularly sexual desire and sociosexual orientation (interest in uncommitted sex). However, published studies seem to agree on no compelling evidence for within-woman changes in sexual desire, sociosexual orientation, mate attraction, or preferences that are associated with fluctuating testosterone or cortisol levels (Jones et al., 2018a, 2018b; Jünger et al., 2018a, 2018b; Marcinkowska et al., 2019; Roney & Simmons, 2013; Shirazi et al., 2019). Regarding between-women effects, it seems that testosterone is linked to individual differences in women's mating psychology. More precisely, partnered women seem to have lower testosterone levels than singles (Edelstein et al., 2011, van Anders & Goldey, 2010), and polyamorous women are reported to have higher testosterone levels than monogamous women (van Anders et al., 2007). Furthermore, testosterone has been reported to be positively associated with sociosexual orientation, general sexual desire, and solitary sexual desire (e.g., masturbation), but negatively to dyadic sexual desire (e.g., sex with a partner, Shirazi et al., 2019; van Anders, 2012). However, neither testosterone nor cortisol seems to be related to interindividual differences in mate preferences (Marcinkowska et al., 2019).

Moderating Variables

One potential reason for mixed findings regarding mate preferences and attraction might be that there are large individual differences in how women react to fluctuating hormones across the cycle (Jones et al., 2019a). Thus, differences in mate preferences or attraction might also be influenced by other variables than women's cycle or fluctuating levels of estradiol and progesterone. Across different hypotheses, one variable that is assumed to potentially affect

mate preferences and attraction is women's relationship status. Women's mating psychology might be sensitive to the presence of a stable investing long-term partner, as benefits of pregnancy might only outweigh its costs when a supportive mate is available to provide care and resources. Thus, changes in mate preferences in line with the GGOSH or changes in mate attraction according to the MPSH might be stronger for or even exclusive to women in relationships. Indeed, a number of studies suggest that relationship status is an important variable, in that mate attraction shifts or shifts in sexual desire only occur for women in relationships (Jünger et al., 2018a, 2018b; Pillsworth et al., 2004). Mate preference shifts have been reported to be stronger either for women in relationships (Penton-Voak et al., 1999) or for singles (Gangestad et al., 2019). However, relationship status did not influence mate attraction (Stern et al., 2021) or mate preferences (Jones et al., 2018a; 2018b; Jünger et al., 2018a, 2018b; Marcinkowska 2018a; Stern et al., 2020, 2021) in the vast majority of studies. Mixed findings might be explained by the fact that effects of relationship status could be more complex than assumed, as relationships differ strongly (e.g., in satisfaction, commitment, length, exclusiveness, and many other factors). Thus, relationship status might not result in the same effect for every woman. Individual differences in effects of relationship status and the exact factors that are accountable for these differences should be examined in future research.

Other variables that have recently been discussed to potentially influence cycle shifts are stress, mood, and premenstrual symptoms (PMS). Stress has been reported to affect reproductive hormones, in that high levels of stress inhibit estradiol levels (Roney & Simmons, 2015), and decrease preferences for masculine faces (Ditzen et al., 2017) as well as attraction to male bodies (Jünger et al., 2018a). However, the latter has not been replicated in a recent, larger study (Stern et al., 2021). Higher perceived stress also seems to be related to lower dyadic sexual desire (Raisanen et al., 2018). Mood has been reported to be related to in-pair, but not extra-pair, sexual desire (Shimoda et al., 2018), whereas it does not seem to be significantly related to ovarian hormones (Schwartz et al., 2012). Further, Kiesner et al. (2020) argue that PMS symptoms, such as cramps or depression, might strongly influence mate selection and should, thus, be investigated as covariates in studies focusing on cycle related changes in women's mating psychology. However, research on how these variables affect changes in mate attraction or preference is overall scarce.

Cues to Fertility

Besides changes in women's sexual interests being a potential cue for men to infer whether they are currently fertile or not, it has been assumed that there might be other, more appearance-related cues to women's fertility. Human females do not display obvious cues to fertility that would be comparable to sexual swellings in chimpanzees and bonobos, our closest primate relatives. However, it is possible that women may show more subtle changes to attract potential mates when fertile, consciously or not. Indeed, numerous studies suggest that women's attractiveness changes across the cycle. The first attempts to examine such potential cues to fertility focused on changes in women's scent and reported that body odor around ovulation is perceived as being more attractive than at other phases of the cycle (e.g., Singh & Bronstad, 2001). This finding has been successfully replicated several times (Gildersleeve et al., 2012; Havlíček et al., 2006; Kuukasjärvi et al., 2004; Thornhill et al., 2003). However, between-women differences might be larger than within-woman differences, and cyclical changes in attractiveness might be too small to be detectable by others (see also Roney, this volume). Other studies have also reported that women's facial or vocal attractiveness changes across the cycle, with women being evaluated as more attractive around ovulation (Pipitone & Gallup, 2008; Roberts et al., 2004), which has also been linked to fluctuating levels in estradiol and progesterone (Puts et al., 2013). Whereas replication studies investigating voice attractiveness across the cycle are sparse, changing facial attractiveness has not been replicated in most subsequent studies (e.g., Bleske-Rechek et al., 2011; Catena et al., 2019; Jones et al., 2018c), casting doubt on earlier reports.

If women's attractiveness really changes across the cycle, what are the cues that change? Previously assumed fluctuating facial cues of fertility were facial shape and skin color (Bobst & Lobmaier, 2012; Burriss et al., 2015; Oberzaucher et al., 2012). However, changes in facial shape do not seem to replicate (Marcinkowska & Holzleitner, 2020) and changes in facial color are apparently too subtle to be detectable by the human visual system (Burriss et al., 2015). Voice pitch (how deep a voice sounds) develops under hormonal influences (Puts et al., 2013) and might thus change across the cycle. Evidence for this claim has been mixed so far, with some studies reporting higher female voice pitch around ovulation (Bryant & Haselton, 2009), no differences in pitch between the fertile and the luteal phase (Banai, 2017), or even lower voice pitch when fertile (Karthikeyan & Locke, 2015). Thus, whether and how women's voice pitch changes across the cycle appears controversial.

Other research suggests cues to fertility that are more actively affected by women's behavior, including changes in clothing style (in that women dress more sexy, provocative, or attractive) and in time spent grooming. Both can

signal sexual interest and attract potential mates. After a first study reported that women try to look more attractive at peak fertility (Haselton et al., 2007), more studies followed reporting that women do or aim to wear more sexy, skin-revealing clothes (Durante et al., 2008; Saad & Stenstrom, 2012; Schwarz & Hassebrauck, 2008), or prefer to buy sexier clothes (Durante et al., 2011). The latter has also been linked to fluctuating hormone levels (Blake et al., 2017a). Further, diary studies suggest that women spend more time grooming when fertile (Röder et al., 2009; Saad & Stenstrom, 2012). The prominent finding that fertile women wear more red or pink clothes (Beall & Tracy, 2013; Eisenbruch et al., 2015; Tracy & Beall, 2014), a color that is potentially worn to enhance attractiveness (Prokop & Hromada, 2013, but see Peperkoorn et al., 2016), failed to replicate in multiple recent studies (Arslan et al., 2021; Blake et al., 2017b; Hone & McCullough, 2020). Summarizing the current evidence, it seems that women's grooming and choice of dress in terms of sexiness might change across the cycle, whereas clothing color does probably not. However, so far there is a lack of large-scale replication studies investigating the robustness of these effects.

Male Mate Retention

If women's sexual interest changes throughout the cycle and there are, indeed, cues to fertility, do their partners recognize any changes? How do they react if their partner is more interested in mating with other men? Indeed, some research suggests a fertile phase increase in men's jealousy, but also in their affection to their partner, effects that predispose mate-retention behavior (Gangestad et al., 2002; Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006). These behaviors have previously been interpreted as counteradaptations to shifts in women's mate preferences and sexual desire in line with the GGOSH. Arslan et al. (2021) did not detect changes in male mate retention, but note limitations of their study design to examine potential shifts. Although it seems plausible that should women's sexual interest show noticeable changes, their close relationship partner shows a reaction, men's perspective and behavioral changes corresponding to female cycle shifts are overall understudied so far.

Hormonal Contraception

If women's mating psychology is affected by changing hormone levels across the cycle, these effects are likely suppressed when taking hormonal

contraception (e.g., the pill; Fleischman et al., 2010). Women taking hormonal contraception do not experience a fertile phase or ovulation and hormone levels are somewhat constant (Alvergne & Lummaa, 2010). Thus, women taking hormonal contraception should not experience changes in their mating psychology across the cycle. In line with this idea, it has been reported that women using hormonal contraceptives do not experience midcycle increases in sexual desire (Arslan et al., 2021). Studies also reported overall weaker preferences for masculine men when women used oral contraceptives (Feinberg et al., 2008; Little et al., 2002). However, these findings were, again, challenged by failed replications, some of which even reported results in the opposite direction (Cobey et al., 2015; Jones et al., 2018b). Further, it has also been proposed that not only mate preferences but also mate choice might be affected by hormonal contraceptives in that women taking the pill might form relationships with men other than whom they would have chosen when not on the pill (Alvergne & Lummaa, 2010). As a consequence, relationship satisfaction, especially sexual satisfaction, as well as jealousy, might change when women switch from oral contraceptive use to none or vice versa after relationship formation. This is known as the pill congruency hypothesis (Cobey et al., 2013; Roberts et al., 2014). Its rationale is that the hormonal pill might affect women's mate preferences in a way that they form a relationship with a partner who does not reflect their preferences after switching to nonhormonal contraception, thus causing a mismatch between preferences and the partner. However, a replication study with a substantially larger sample size than the original studies did not find support for the pill congruency hypothesis (Jern et al., 2018).

Most of the mentioned studies relied on between-subject designs, which are confounded by potential selection effects, thus, differences between women taking the pill and non-pill users, which could interact with the investigated variables. To draw reliable inferences on how the pill affects women's mating psychology (as well as other outcomes), researchers should ideally employ either within-subject designs (assessing the same women while taking the pill vs. while naturally cycling) or blind randomized control trials (with some women randomly assigned to take the pill versus other women to take a placebo; Alvergne & Lummaa, 2010). Since such studies are difficult to conduct, it is mandatory that appropriate statistical techniques are carefully applied in order to correct for confounding selection effects.

Methodological Criticism and Potential Reasons for

Nonreplicability

Many of the originally reported findings we review in this chapter failed to replicate in later studies, causing uncertainty whether these effects actually exist. How is it possible that different studies find different results regarding the same research question? There is no single reason for nonreplicability, but several problems that might collude. First, many studies in this area are underpowered, which means that they did not investigate enough participants and/or assessments within participants to draw reliable conclusions. Underpowered studies can cause false negative (e.g., failure to detect an effect that exists) but also false positive (e.g., support for an effect that does not exist) results. For example, Jones et al. (2019a) conclude that the mean sample size of studies reporting mate preference cycle shifts for men's faces before 2018 was only forty participants, although an independent power analysis suggests that these studies (with their specific methods) would have required 900–1,000 participants to reliably detect a medium-size effect (Gangestad et al., 2016). Second, most of the studies before 2018 have used between-subjects designs, but their results have been interpreted as within-subject effects. As mentioned above, it is possible that mate preferences do, indeed, vary between women rather than within woman. Thus, between-subject designs are potentially confounded. Furthermore, between-subjects studies need an even larger sample size than within-subjects studies to have appropriate test power for cycle shifts (Gangestad et al., 2016). Third, most studies relied on measures to estimate the fertile window with suboptimal validity: Self-report data and counting methods to define the fertile days instead of validating their estimates with luteinizing hormone urine tests to pinpoint the day of ovulation, with the defined number of fertile days ranging widely from three to twenty days. Ovarian hormones were not directly assessed in most studies. However, even if they were, hormone assays are increasingly under scrutiny regarding their own validity problems (Schultheiss et al., 2019). Fourth, variation in methods across studies can cause nonreplicability (e.g., for stimulus presentation, using natural vs. artificial stimuli, different items, or sampling designs). Direct replications are rare. Fifth, researcher degrees of freedom and analytical flexibility, the fact that all researchers have to choose how exactly to conduct their study, formulate their hypotheses, analyze their data, and report their results, from a wide range of reasonable and defensible options (Wicherts et al., 2016), as well as publication bias in favor of positive findings attenuates replicability. Importantly, most of these issues are not exclusive to ovulatory cycle research, but are widespread across most scientific fields.

So which studies can we rely on? All studies come with limitations, and no single study should be regarded the final word on any research question. Robust effects should replicate across different methodological approaches and analytic decisions (Stern et al., 2019). However, identical analytic decisions should also lead to similar results across different, comparable datasets (Stern et al., 2021). Every new dataset contributes valuable new information and should be used to reevaluate the overall picture. This is especially true for well-powered replication studies, be it direct or conceptual replications. It is crucial to note that ovulatory cycle effects occur within subjects and are thus best studied using within-subject data, as between-subject studies require samples more than an order of magnitude larger to yield comparable power (Gangestad et al., 2016). It should also be noted that a lot of the older studies in this literature, which were more likely to report significant effects and larger effect sizes (as initial studies on a topic often do, the so-called winner's curse; Young et al., 2008), had critically low power (Jones et al., 2019a) and should thus be weighted accordingly. High power, coming from both more subjects and more assessments per cycle within subjects, are especially important when testing higher-order interaction effects (which are often predicted in this literature) since interactions are especially prone to yield false-positive results (Rohrer & Arslan, 2020). Studies in this literature also vary widely with regard to research transparency, including preregistration (or ideally registered reports), open data, scripts and materials, and supplementary robustness analyses. Given that there have been considerable analytic developments in this area (e.g., multilevel modeling and regarding the estimation of fertility) and that this literature has already sparked debates over the analysis of individual open datasets, making more of the data in this area open for reevaluation would greatly benefit the field. Finally, more data are always helpful, especially on effects that have seen few replications so far, like the luteal shifts in eating behavior predicted by the MPSH.

Summarizing the current evidence

Hormones, including fluctuations across the ovulatory cycle, seem to have some impact on women's mating psychology, but probably less so or differently than previously assumed. The recent years saw a lot of methodological developments, failed large-scale replications, debates over studies that allowed for it via their transparency, and the emergence of new alternative hypotheses. Though it is too early to confirm which hypothesis explains hormonal influences on women's mating psychology best, some findings seem to be more robust than others (e.g., that sexual desire and women's odor vary across the cycle). These

rather robust findings suggest that estrus is not completely lost but is also not overtly advertised in human females. Future studies should also investigate whether there are potential individual differences among women in the degree in which they show ovulatory shifts in their mating psychology, or whether some women show such shifts whereas others do not. Overall, more research is needed to clarify how exactly women's hormones and ovulatory cycles affect their mating psychology.

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CHAPTER
32

The Impact of Hormonal Contraceptives on Women's Sexual and Mating Psychology

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Abstract

Women's sex hormones play an important role in shaping women's mating psychology and behavior. These hormones are disrupted by the use of hormonal contraceptives (HCs), which suppress the release of women's own dynamically changing ovarian hormones and supplant them with a consistent dose of synthetics. Although a majority of reproductive-aged women have used HCs to manage fertility at some point in their lives, little is known about the impacts of the artificial hormones in HCs on women's mating psychology and behavior. In the current chapter, we review what is known and not known about the relationship between HC use and women's mating and sexual psychology. The chapter closes by addressing important limitations of the existing research and delineating fruitful areas for future study.

Key Words: Contraceptives, Hormones, Mating, Sexual Psychology, Fertility, Female Sociality

If you were to take a poll of reproductive-aged women and asked them about the most important issues on their mind when it comes to sex and mating, there is little doubt that pregnancy prevention, or birth control, would fall near the top of the list. For modern women, the ability to safely and effectively regulate fertility is paramount to being able to enjoy having romantic and sexual relationships with men, while still being able to meet long-term career and educational goals. Perhaps not surprisingly, 98 percent of women in the United States report having used birth control at some point in their lives, and 62

percent of reproductive-aged women report using some form of birth control right now (Hurt et al., 2012).

Although pregnancy prevention is an issue confronting sexually active men and women alike, the costs of failing to prevent unwanted pregnancies are greater for women than they are for men (Alkema et al., 2016; Trivers, 1972). This is because women are the ones who must physically endure the costs of pregnancy or a pregnancy termination, both of which can be substantial. A full-term pregnancy lasts nine months and—despite our advanced medical technology—childbirth continues to kill 211 women per 100,000 live births each year (World Health Organization, 2019). An additional 68,000 women die each year due to complications that arise from lacking access to safe, legal abortions (Haddad, 2009). Women are therefore overwhelmingly more motivated than men to bear the responsibility of birth control within their sexual dyad; they simply have more to lose.

Although there are multiple forms of female-led contraception, one of the easiest to use and most effective is the birth control pill. It is also among the most popular. Eighty-two percent of women report having used the birth control pill at some point in their lives, and that number jumps to 88 percent if you include all forms of hormonal contraceptives (National Center for Health Statistics, 2019). Despite the popularity of hormonal contraceptives (HCs), little is known about the full spectrum of their psychological impact on women. This is particularly true in the domains of sex and attraction, about which there are several conflicting reports about what HCs do and do not do to the brain and behavior. In this chapter, we provide an overview of what is known and not known about the impact of HCs on women's mating and sexual psychology. We will close the chapter with recommendations for future research on these topics.

Hormones and Hormonal Contraception

Women's sex hormones have been shaped by selection to coordinate two broad evolutionary objectives: (1) promote sexual behavior and conception, which are activities orchestrated primarily by the sex hormone estrogen, and (2) promote implantation and pregnancy, which are coordinated by the sex hormone progesterone. Estrogen rises steadily during the first ten to twelve days of a woman's cycle until ovulation. After ovulation, it decreases sharply, followed by a gradual increase for the remainder of the cycle until menstruation is about to occur (Weschler, 2002). Progesterone is the dominant sex hormone during the second half of the cycle, and it gets released by a temporary endocrine structure formed by a vacated egg follicle (the corpus luteum). Progesterone rises steadily

during the second half of the cycle (the luteal phase) in anticipation of implantation and pregnancy but then falls sharply, triggering menstruation, when a fertilized egg does not implant (Losos et al., 2002).

Women's ovulatory cycles—and the accompanying rise and fall of each estrogen and progesterone—are coordinated by the hypothalamic–pituitary–gonadal axis (HPG axis). The HPG axis is regulated by a series of feedback loops that are sensitive to women's cyclically changing levels of sex hormones (Dagklis et al., 2014; Wintermantel et al., 2006). When levels of both estrogen and progesterone are low, in addition to triggering menstruation, this prompts the release of follicle stimulating hormone (FSH) and luteinizing hormone (LH) from the pituitary gland via the hypothalamus. These pituitary hormones stimulate the ovaries to mature egg follicles and, ultimately, prompt ovulation. Conversely, when levels of estrogen and (especially) progesterone are high, this inhibits the release of FSH and LH by providing an internal, hormonal cue that ovulation has recently occurred and that it is possible that a fertilized egg may soon implant.

It was the inhibitory effects of progesterone on the HPG axis that served as the inspiration for birth control pills. Birth control pills and other HCs prevent pregnancy by providing a daily dose of synthetic progesterone (called a progestin) and estrogen that mimic the HPG axis inhibiting effects of progesterone and estrogen. By inhibiting release of FSH and LH, they prevent the maturation of egg follicles and the subsequent ovulatory cascade. This means that women's levels of endogenously synthesized estrogen and progesterone stay very low, an egg is never ripened and released, and women don't have to worry about the possibility of pregnancy (Nelson & Cwiak, 2011).

Because the synthetic hormones that are in HCs have been designed to inhibit the release of FSH and LH by stimulating progesterone receptors (in a way that is similar to what occurs in naturally cycling women during the luteal phase of the menstrual cycle), it is intuitively appealing to assume that HC-taking women's psychology and behavior will be similar to that of naturally cycling women at times when progesterone is dominant (see, e.g., Baker et al., 2001). That is, given the hormonal message created by HCs, it would be reasonable to predict that the brains and bodies of HC-taking women would do some of the same types of things that naturally cycling women's bodies do when they are in the progesterone-dominant phase of their cycle. However, as of this writing, there is very little known about the degree to which the hormonal message created by the synthetic hormones in HCs is similar or different from the hormonal message created by women's own hormones. For example, although researchers know for certain that the synthetic hormones used in HCs inhibit

release of FSH and LH and maintain the endometrium, the full extent to which the artificial hormones in HCs influence the other cells in the body that have hormone receptors for progesterone and estrogen isn't currently well understood. Although there is reason to expect that the hormonal message being created by HCs is similar to what is observed in naturally cycling women in the luteal phase of the cycle, there are also likely to be important differences stemming from structural disparities between the progestins used in HCs and endogenously produced progesterone.

For example, although the synthetic estrogen (ethinyl estradiol) that is used in HCs is synthesized from estrogen, the majority of synthetic progestins in use are synthesized from testosterone (Sitruk-Ware, 2008). These testosterone-based progestins are similar enough to progesterone that they are able to stabilize the endometrium and inhibit the hormonal cascade that ultimately prompts ovulation. However, differences between these exogenous progestins and endogenous progesterone may also lead to unintended physiological and psychological side effects. For example, many of the progestins that are synthesized from testosterone are known to activate testosterone receptors, resulting in masculinizing psychological effects in women (McFadden, 2000), such as decreased verbal fluency and increased performance on mental rotation tasks (Griksiene & Ruksenas, 2011). Accordingly, although it is a useful starting point to predict that HC-using women will be more psychologically and behaviorally similar to naturally cycling women in the luteal phase than in the periovulatory phase, the two hormonal messages aren't equivalent. Therefore, the study of HCs on women's psychology and behavior needs to assume that HC-taking women will be different from natural cyclers at any point in their cycle. We cannot make the assumption that the psychological and behavioral patterns that are observed in response to HCs might serve an adaptive function that would have historically helped promote fitness in the context of the luteal phase. Instead, we need to approach the psychological and behavioral patterns observed among women on HCs as being biologically distinct, resulting from a hormonal state that has no natural biological equivalent.

Hormonal Contraceptives and Sexual Psychology

One of the areas that has been most well researched with respect to the effects of HCs on women's mating psychology are the effects of HCs on women's sexual desire and sexual functioning. For instance, research finds that HC-taking women rate themselves as being less passionate and romantic (Nowosielski et al., 2019), tend to initiate and have sex less frequently (Adams et al., 1978;

Caruso et al., 2004), and exhibit lowered libido (Wallweiner et al., 2010) compared to naturally cycling women (although some researchers have found the opposite; Pastor et al., 2013; Schaffir, 2006). Others find that HC-using women are more likely to have problems with pain or discomfort from sex than naturally cycling women (Wallwiener et al., 2015), and a recent meta-analysis of twelve studies consisting of more than nine thousand women found that women on HCs report having significantly lower sexual desire than women not using HCs (Huang et al., 2020).

Despite the mounting body of evidence suggesting that HCs may impair sexual desire and sexual function, it is unlikely that these effects are unilateral, affecting all women who use them in the same way. Instead, it is likely that the relationship between HC use and sexual functioning is highly person dependent, varying as a function of women's unique biological responses to the hormones in their HCs. For example, in one large review of thirty-six studies, the researchers found that 63.6 percent of HC users reported no change in sexual desire, 21.7 percent reported an increase in sexual desire, and 14.7 percent of users reported a decrease in sexual desire (Pastor et al., 2013). Note, though, as do the authors in the body of their review, that many of the papers finding no changes in libido were supported by the HC industry. Nonetheless, additional research is needed to examine the range of effects that HCs have on women's sexual desire and functioning and to identify the factors responsible for these differences.

In addition to the impact that HCs can have on women's sexual desire and function, some research suggests that the impact of HC use on women's sexual psychology may operate at very early stages of cognition, impacting women's attentional systems. For example, in one study, researchers had HC-taking and naturally cycling women look at almost one-hundred sexually explicit photographs while wearing an eye-tracking device (Rupp & Wallen, 2007). They then measured the aspects of the photographs that most captured and held the women's attention. The results revealed that the HC-taking women were quicker to lose interest in the sexual imagery than were their naturally cycling counterparts. Instead of spending most of their time looking at the models in the photographs—which is what naturally cycling women did—their attention quickly drifted away from the sexual scene to focus on irrelevant objects in the background, such as the furniture or artwork. Although additional research needs to be done to test the robustness of these patterns, these results suggest that, for some women, HC use may lower sexual motivation, even at a preconscious level.

There are several reasons why HC use can have a negative impact on women's sexual functioning, many of which are caused by the hormonal

differences observed between naturally cycling and HC-using women. In particular, differences in levels of estrogen and testosterone are reasoned to play an important role in the differences observed between these two groups of women. For women, sexual motivation is fueled, in large part, by estrogen (Adams et al., 1978; Pillsworth et al., 2004). Accordingly, suppressing ovulation and, as a result, keeping women's levels of estrogen low and stable across the cycle can contribute to reductions in libido and lower sexual functioning than what is typically observed in naturally cycling women (Shirazi et al., 2019).

A second mechanism through which HC-taking women can experience reductions in libido and sexual functioning is through differences in levels of testosterone (T) that are observed between HC users and natural cyclers. Just as it does with men, T plays an important role in women's sexual function (Roney & Gettler, 2015). T impacts sexual arousal and sexual responsiveness, and it is necessary for the body to synthesize estrogen, which is the other major driver of women's sexual motivation. Unfortunately for HC-using women, a substantial body of research shows that HCs can cause steep declines in women's levels of free, unbound T (Aden et al., 1998; Coenan et al., 1996; Edwards & O'Neal, 2009). For example, one recent study found that HC users' free T levels are an average of 61 percent lower than naturally cycling women's (Zimmerman et al., 2013).

HC use can cause this effect in two ways. First, HC use reduces the amount of T produced by the ovaries and adrenal glands (Fern et al., 1978; Madden et al., 1978; Carlström al., 2002). Second, the synthetic hormones in HCs increase levels of sex hormone binding globulin (SHBG; Vange et al., 1990; Wiegratz et al., 2003), which binds to T and makes it inactive. Thus, the already diminished levels of free T in HC-using women are even further reduced by HCs' effect on SHBG. Although some researchers find that the relationship between HC-related decreases in T and sexual motivation are small or altogether absent (see, e.g., Alexander et al., 1990; Graham et al., 2007), others find that that these differences can cause meaningful decrements in women's sexual functioning (van Anders, 2012; Warnock, 2006). For example, in one recent review of the literature, researchers found evidence linking HC-induced decrements in T and increments in SHBG to reduced sexual desire in half of the thirty-six studies they reviewed (Pastor et al., 2013).

It is not just baseline levels of T that appear to be affected by HC use; women's T *response* to sex-relevant stimuli also seems to be affected. For example, in one study, researchers had women watch a love scene from *The Notebook* or one of three sex-irrelevant control videos (López et al., 2009). Although sexual stimuli typically prompt the release of T, HC-taking women

exhibited a significantly blunted T response to the sexual scene compared to what was observed in naturally cycling women. This was true despite the fact that HC-using women's T was significantly lower to begin with. Others conducting similar studies have found that HC-taking women's T *decreases* in response to sexual scenarios (Goldey & Anders, 2011). These findings indicate it is not just that women using HCs are less interested in sex but that changing their hormonal profiles impacts the body's neuroendocrine response beyond its intended targets.

Finally, research in nonhuman animals suggests that HC use might also lead to decreased concentrations of allopregnanolone in the brain (Porcu et al., 2012; Santoru et al., 2014). Allopregnanolone is a neurochemical involved in mood and memory that also plays an important role in motivating sexual behavior. This is yet another biochemical change induced by HCs that might have a negative effect on HC-using women's desire for sex. Other hormones and their related psychological outcomes may also be impacted by HC use; however, little is known about the full range of physiological effects of synthetic estrogen and progestins.

Hormonal Contraceptives and Sexual Attraction

Researchers have been, for decades now, examining the links between hormonal fluctuations that occur across the ovulatory cycle and women's partner preferences, sensory acuity, and relationship dynamics (see, e.g., Caruso, 2001; Durante & Arsena, 2015; Larson et al., 2013; Meltzer, 2017). For example, when estrogen is dominant, research finds that naturally cycling women prefer the scent of symmetrical men (Gangestad & Thornhill, 1998; Havlíček et al., 2005), men with masculine faces (Johnston et al., 2001; Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; Roney & Simmons, 2008), deeper, more masculine male voices (Feinberg et al., 2008; Puts, 2006), and men who are socially dominant and confident (Gangestad et al., 2004; Lukaszewski & Roney, 2009), compared to what is observed at nonfertile points in the cycle. Although several highly powered and well-designed studies have failed to find an effect of ovulatory cycle phase on women's mate preferences (see, e.g., Jones et al., 2018; Jünger et al., 2018; Marcinkowska et al., 2018; Marcinkowska et al., 2019; Wood et al., 2014), the number of studies that have found effects suggests that the hormonal fluctuations associated with conception risk may have an important impact on some women's mating psychology.

Women who are on HCs, of course, do not exhibit the cyclical changes in sex hormones that are observed in naturally cycling women. Instead, women on HCs

receive the same hormonal message every day, and it is a message that consists of relatively low levels of estrogen and relatively high levels of progestins. Consistent with what is observed in research linking estrogen levels to a heightened preference for facial masculinity (Roney & Simmons, 2008), women on HCs have sometimes been found to exhibit a preference for less masculine faces and voices, similar to the preferences exhibited by naturally cycling women in the luteal phase (Jones et al., 2005).

For example, in one set of studies, naturally cycling women created their ideal short-term and long-term partners by clicking a computer mouse to masculinize or feminize a digital male facial prototype (Little et al., 2013). After this, half of the women began using HCs while half continued naturally cycling. When the women completed the task a second time after three months, the naturally cycling women showed no difference in their preferred masculinity of men's faces. However, the women who began taking HCs created significantly less masculine ideal male faces for both short- and long-term partners compared to before they started using HCs. The researchers also found that this preference impacted women's actual partner choices. Men in relationships—with women who were either taking HCs or not at the time they began the relationship—were photographed and rated on their subjective (rated by third-party observers) and objective facial masculinity (calculated by cheekbone prominence, the ratio of jaw height to lower face height, and face height to width). Results revealed that HC-using women chose less masculine men to be their romantic partners than non-HC users. Although others have failed to replicate this pattern using different methods (Jones et al., 2018), these results suggest that women's preference for facial masculinity may change in response to HC use. Given the mixed results in this area, however, future research is needed to determine whether these patterns stand the test of time.

Despite the lack of consensus on the links between HC use and women's expressed preference for masculine men, research in neuropsychology and psychophysics are consistent with the idea that HC users may prioritize different qualities in their partners than natural cyclers. For example, research finds that women who are on HCs exhibit less activity in the reward centers of the brain when looking at masculine faces (Montoya & Bos, 2017) than do naturally cycling women, whereas others have found that HC users exhibit *more* brain activity in these same centers in response to monetary rewards (Bonenberger et al., 2013). This latter pattern is reasoned to reflect a preference for stimuli related to investment and relationship commitment, both of which are reasoned to be greater in the context of progesterone-dominated states such as that created by HCs (Mazur & Michalek, 1998; McIntyre et al., 2006; Roney et al., 2006).

Given the importance of allomaternal provisioning in the survivability of women's offspring and their reproductive success (Hrdy, 2016; Isler & van Schaik, 2012), the preference for cues to material investment is reasoned to have been beneficial to women at all points in the cycle, particularly at times in the cycle with the hormonal signature mimicked by HCs.

In the area of psychophysics, research finds that HC use may blunt women's sensory acuity in ways that diminish their ability to distinguish between men who have markers of high genetic quality and genetic compatibility, and those who do not. For example, research examining women's sensitivity to testosterone metabolites and male body odors found that naturally cycling women were more sensitive to these scents than women on HCs (Renfro & Hoffman, 2013), particularly when compared to naturally cycling women in the periovulatory phase of the cycle. This suggests that HC use may decrease women's ability to detect subtle scent-based differences between men that ovulating women can easily pick up on. Indeed, research finds that HC use disrupts disassortative odor preferences that typically shape naturally cycling women's preferences for genetically dissimilar men (Roberts et al., 2008; Sorokowska et al., 2018; Wedekind et al., 1995). For example, couples using HCs are more genetically similar than non-using couples (Allen et al., 2019), suggesting a possible blunting of such sensory acuity. Although it is possible that HC-taking women simply place less of an emphasis on cues to high genetic quality and compatibility than do naturally cycling women, failure to distinguish between men with and without these cues indicates a lack of attunement to these features at all. Because HC-taking women are in a perpetual state of nonovulation, their sensory acuity may not be attuned to genetic quality and compatibility cues in the same way that naturally cycling women are.

The impact of HC use on partner preferences may also manifest itself as differences in relationship and sexual satisfaction between naturally cycling women and HC users. For example, in one study, researchers examined whether there were observable differences in relationship quality between women who had met their partners while they were naturally cycling or using HCs. They found that women who chose their partners when they were naturally cycling felt more satisfied with their sex lives than women who chose their partners while on HCs (Roberts et al., 2011; Russell et al., 2014). Despite the detriment to sexual satisfaction, women who chose their partners while on HCs reported higher relationship satisfaction in general (Taggart et al., 2018), were more satisfied with their partners' financial provisioning ability and intelligence, and were significantly less likely to get divorced than the women who chose their partners when naturally cycling (Roberts et al., 2011). Others have found HC use to be

associated with lower sexual enjoyment for women *and* their partners (Blumenstock & Papp, 2019); however, this latter decrement is not observed in HC-taking women who were also on HCs prior to meeting their partner (Roberts et al., 2014).

In addition to potentially impacting women's partner preferences in ways that have implications for relationship satisfaction and the divorce rate, research suggests that changing a woman's hormonal landscape during the course of a relationship may also have consequences for relationship satisfaction. For example, research finds that women who were not using HC when they chose their partners but *then* went on it reported a decrease in sexual satisfaction as a result of starting HC (French & Meltzer, 2020). This is consistent with the body of research that finds libido-harming side effects of HC use. However, researchers have also found similar changes in sexual satisfaction among women who were on HCs when they met their partners but then discontinued use. For these women, though, whether these changes were positive or negative depended on their husband's facial attractiveness (Russell et al., 2014). For women with attractive husbands, stopping HC use increased their sexual satisfaction. But for women with unattractive husbands, stopping HC decreased sexual satisfaction. Others have found similar results, demonstrating that after discontinuing HCs, partnered women pay more attention to and express greater interest in engaging in sexual activity with attractive men (Birnbaum et al., 2019) compared to women who met their partner when they were not on using HCs.

Although others have failed to find evidence that starting or discontinuing HCs impacts relationship quality (see, e.g., Jern et al., 2018), those who have found these effects have reasoned that they emerge in response to the different qualities that HC-using and naturally cycling women generally emphasize in their partner choice. That is, because HC-using women tend to exhibit a diminished preference for cues to masculinity relative to what is observed for naturally cycling women (Jones et al., 2005; Little et al., 2013), it has been reasoned that changing HC status could increase or decrease women's relationship satisfaction depending on the degree to which their previously chosen partner conforms to the preferences of their new hormonal state. Given the inconsistent support for this hypothesis, however, additional evidence is needed before conclusions can be drawn about the relationship between changing HC status and women's sexual and relationship satisfaction.

Finally, research comparing oxytocin signaling differences between HC users and nonusers also provides hints to the mechanistic underpinnings behind differences between HC users' and natural cyclers' relationship satisfaction (Garforth et al., 2020). Oxytocin is a hormone that functions to boost social

bonds and is released in response to loved ones, including children and romantic partners (Schneiderman et al., 2012). Because oxytocin promotes romantic emotions, if a person is administered a dose of intranasal oxytocin, it will generally cause them to see their romantic partner as being more attractive than other people they're looking at (Behnia et al., 2014). In naturally cycling women, it also causes the reward centers of the brain, such as the nucleus accumbens, to activate in response to seeing their partner. However, HC users experience no such effect when given a dose of intranasal oxytocin (Scheele et al., 2016). HC-taking women also don't experience increased activity in the reward centers of their brain when looking at pictures of their partners. Instead, when HC-taking women view photographs of their partners, they respond as if looking at the face of a stranger. The normal biological process that results as a response to oxytocin that helps label a romantic partner as someone special and flags him as a reinforcing stimulus doesn't occur in HC-taking women. Overall, HC use has a broad impact on human mating psychology that affects not only women's sexual behavior and cognition but men's as well.

Hormonal Contraceptives and Men

Estrogen, because of its strong links to fertility, is associated with physical and psychological states that promote conception in women. However, given that men would also benefit from modulating their mating related efforts based on a female partner's fertility status, men's mating psychology should also be attuned to fertility cues, raising the possibility that HC use might also impact the psychology and behavior of *men.*

For example, in one study, researchers tracked lap dancers' tip earnings over two months, half of whom were naturally cycling and half using HCs (Miller et al., 2007). Because men tend to give higher tips to the dancers they prefer, the researchers could test whether men find women more desirable at high fertility by looking at how much tip money they earn across the cycle. The results of this study found that the dancers earned around $70 per hour when they were near ovulation. They earned around $35 per hour during their periods, when they were nonfertile. And they earned around $50 at other times, when fertility was waxing and waning. Women on the pill averaged around $37 per hour, with no peaks and valleys, like those observed by the naturally cycling women. Whether these effects are attributable to the dancers' physical attractiveness across the cycle or their behavior when conception risk was either high or low is unclear. Regardless, these findings reflect that men are most sexually interested in fertile women, particularly when conception risk is highest. It is reasoned that these

patterns reflect men being attuned to cues that would have facilitated successful gene transmission.

The effects of women's HC use on men's mate preferences are also found in men's sense of smell. Several studies find that women's natural body scents collected at high fertility are rated by men as being more desirable and pleasant than scents collected at low fertility (Gildersleeve et al., 2012; Havlíček et al., 2006; Woodward et al., 2015). Men also may exhibit a hormonal response to women's bodily odors, with a rise in T when smelling t-shirts worn by women during ovulation and decrease in T when smelling t-shirts worn during the nonfertile luteal phase (Miller & Maner, 2010). This indicates that hormonal cues from women may instigate a complementary hormonal reaction from men. Although this latter effect has failed to replicate in a carefully controlled replication attempt (Roney & Simmons, 2012), other studies have replicated this pattern. For example, research finds that men's levels of T (and cortisol) increase in response to breathing in air infused with scents collected from women's armpits and vulvas at high fertility compared to low fertility (Cerda-Molina et al., 2013). The men also reported being more interested in sex after smelling the high-fertility scents compared to the control or low-fertility scents.

Finally, research suggests that men might also change their partner-related behaviors depending on their partner's HC use. For example, in one study, researchers examined a sample of newlywed couples to look at the connection between women's relationship commitment and the mate-guarding behaviors of men (French et al., 2017). The results revealed that commitment on the part of wives predicted mate guarding by their husbands, unless the men were married to a woman using HCs. For men married to women using HCs—although there was an association between a wife's low commitment and a husband's jealousy—there was no increase in mate-guarding behaviors (which was what was observed for men partnered to naturally cycling women). So, even though these men felt more jealous than men with more committed partners, they took fewer actions to do anything to keep their partner away from other men**.** Together, these results suggest that men do not expend as much energy protecting their mates or pursuing new mates that are using HCs as they would if the women were naturally cycling.

What We Still Need to Know

Whereas hormonal contraceptives have been a major advancement for women, the research presented here shines a light on the many unintended consequences of taking HCs on patterns of human mating behavior. Although

many doctors describe HCs as a targeted form of birth control, it is evident that HCs have several physiological and psychological effects beyond the reproductive organs themselves. However, relatively little is known about all of the ways in which HCs affect women's health, cognition, and behavior. Here, we offer some of the most pressing issues yet to be explored when it comes to HCs' impact on women.

One of the most pervasive limitations with the existing literature on HC use and psychological outcomes is related to study design; longitudinal work is needed to adequately examine the changes caused by HC use and discontinuation *within* women. Currently, the majority of research on the psychological effects of HCs utilize a cross-sectional, correlational study design and only examine differences *between* women. While this research has provided important insights into the relationship between HC use and differences in the structure and function of the brain and behavior, future work should prioritize using experimental, longitudinal approaches to understand the causal impact of HC use on these outcomes within individual women. Although randomized experiments using HCs as a manipulation present many practical and ethical challenges, such challenges are likely worth overcoming, given the pervasive use of HCs among women and the pervasive impact they appear to have on women's psychology.

A second, related limitation to the existing research is one of sample size. Although things have improved markedly since researchers first started to examine the psychological impact of HC use on women, there remains much room for improvement. The literature, as it stands, makes it very difficult to draw conclusions about the real psychological impact that HCs have on women. Future research must take seriously the charge to recruit larger samples of women. Given that women's psychological responses to HCs are highly variable, increasing sample size will provide an important starting point for better understanding the individual-level variables that interact with HC use to impact a woman's mating preferences and behaviors.

Another area that is in urgent need of research attention is the long-term physiological and psychological impact of HC use during adolescence. Because estrogen and (although to a much lesser extent) progesterone play an important role in shaping pubertal sexual development, it is possible that preventing the normal hormonal fluctuation of sex hormones that begin at menarche could have a lasting impact on women's physiological and psychological development (Gray et al., 2010; Zhang et al., 2008). Increasing numbers of young women are beginning to use HCs as young as twelve years old (Cromer et al., 2004), but little remains known about the developmental impact this practice has on

women's brain development. It is imperative that future research examine, longitudinally, the impact of HC use during adolescence on women's sexual and psychological health.

Finally, future research should focus on how different formulations of HCs and methods of delivery (pill, implant, shot, etc.) differentially impact behavior. There are nearly a hundred different formulations of HCs with differing levels of progestins and estrogen, meaning the hormonal message signaled by each combination will be slightly different. Given that several cognitive and behavioral shifts have been observed in relation to women's ratio of estrogen to progesterone throughout the cycle (Asarian & Geary, 2006; Durante et al., 2011; Jones et al., 2005; Roney & Simmons, 2013), the psychological impacts of differing hormonal compositions across types of HCs are deserving of exploration. Moreover, progestins alone vary from HC to HC. There are four types of progestins, and women's responses to each type may be different (Goldstuck, 2011). For example, in one study examining the relationship between progestin type and depression, a common symptom of HC use, the risk of depression varied depending on the type of progestin used and the mode of delivery (Worly et al., 2018). There is no reason to expect that HCs' impact on mating psychology will be any less nuanced and progestin- and delivery mode-dependent. Indeed, we believe that these differences are likely responsible for at least some of the failures to replicate research findings in this area.

Despite the limitations of the existing research—and the number of questions it raises—the current work suggests that HCs are likely to have an important impact on nearly all facets of human mating behavior. Given the ubiquity of HC use among women—particularly during times in their lives when they are initiating various types of romantic and sexual relationships—there is an urgent need to better understand the impact of these drugs on women and their partners. It is our hope that the next decade will yield these much-needed insights, granting women the opportunity to make informed decisions about their sexual and relationship health.

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PART VII

Mating in the Modern World

CHAPTER
33

Mating in the Digital Age

Helen E. Fisher and Justin R. Garcia

Abstract

Charles Darwin identified two basic forms of sexual selection: intrasexual selection, in which members of the same sex of a species evolved biobehavioral mechanisms to compete with one another to win mating opportunities with the opposite sex—male–male competition and female–female competition—and intersexual selection in which members of each sex of a species evolved biobehavioral mechanisms to attract members of the opposite sex for the purpose of mating—mate choice. Miller proposed that two aspects of mate choice have evolved in tandem: (1) traits of the *display producer* that evolved to attract mating partners and (2) traits of the *display chooser* that evolved to discriminate between specific courtship displays and prefer those of specific display producers. Fisher has proposed that a third mechanism evolved in tandem with hominin mate choice: the brain system for romantic love. Regardless of *whom* the *display chooser* chooses, this corresponding neural mechanism provides the focus, motivation, optimism, and energy to pursue this preferred mating partner. This chapter first reviews current data on this mechanism of mate choice, romantic love. Then, using a sample of 39,913 single adult Americans, the chapter discusses four broad temperament dimensions that play a role in mate choice today; and using a sample of 28,128 single Americans, it discusses three biologically based patterns of mate choice associated with these four neural systems. Last, using a national representative sample of 55,000 single adult Americans, the chapter discusses contemporary patterns of mate choice that most likely evolved during hominin evolution.

Key Words: romantic love, temperament, mate choice, fMRI, Singles in America, slow love

"It's better to be looked over than overlooked."

—Mae West

Premise

Charles Darwin (1871 identified two basic forms of sexual selection: *intrasexual selection*, in which members of the same sex of a species evolve biobehavioral mechanisms to compete with one another to win mating opportunities with members of the opposite sex—known as male–male competition and female–female competition—and *intersexual selection*, in which members of each sex of a species evolve biobehavioral mechanisms to attract members of the opposite sex in order to attain mating opportunities—generally known as mate choice. Darwin's theoretical framework remains intact and relevant to contemporary studies of evolution and mating. This chapter focuses on human mate choice in today's digital age.

The phenomenon of mate choice is so common in nature that the ethological literature regularly uses several terms to describe it, including *mate preference*, *individual preference*, *favoritism*, *sexual choice*, *female choice*, and *selective proceptivity* (Andersson, 1994). Evolutionary psychologist Geoffrey Miller (2000) has proposed that mate choice has two basic aspects that evolved in tandem: (1) traits that evolved in the *display producer* to attract mating partners of the opposite sex and (2) corresponding neural mechanisms in the *display chooser* to discriminate between various courtship displays, become attracted to traits of specific individuals, and pursue preferred potential mating partners. Anthropologist Helen Fisher has proposed that a third mechanism evolved in tandem with hominin mate choice: the brain system for romantic love. Regardless of *whom* the display chooser chooses, this corresponding neural mechanism provides the focus, energy, and motivation to pursue this preferred mating partner (Fisher, 2006; Fisher et al., 2006).

This chapter first reviews the primary neural mechanism that facilitates mate choice in humans, commonly known as romantic love. Using a sample of 39,913 single adult Americans, the chapter then presents data on four broad evolved temperament dimensions that play a role in mate choice today (Fisher, 2009, 2012; Brown et al., 2013; Fisher et al., 2015), and using a sample of 28,128 singles, it discusses three biologically based patterns of mate choice associated with these four neural systems. Last, using a national US sample of 55,000 single adult Americans, the chapter discusses several traits that contemporary human display producers present and choosers prefer in a partner, specifically,

indicators of genetic quality that most likely evolved in the environment of evolutionary adaptedness (EEA), perhaps with the emergence of hominin serial, social monogamy and concomitant clandestine adultery 4.4 million years before present (Fisher, 2011, 2016; Gray & Garcia, 2013).

Romantic Love: The Primary Neural Mechanism of Mate Choice

Romantic love is a cross-cultural human phenomenon associated with a specific suite of biobehavioral traits. These include focused courtship attention on a *specific* partner; intense energy; ecstasy; mood swings; bodily reactions including "butterflies in the stomach" and anxiety; emotional dependence; separation anxiety; frustration-attraction; intrusive, obsessive thinking about the specific beloved; sexual possessiveness; craving for emotional union with the beloved; and extreme motivation to win this *preferred* mating partner (see Fisher, 1992, 2004, 2009, 2011, 2016).

Several neuroimaging studies indicate a primary neural system associated with human romantic love (Bartels & Zeki, 2000; Fisher et al., 2003; Fisher et al., 2005; Aron et al., 2005; Ortigue et al., 2007). And "courtship attraction" among other mammals has neurological similarities human romantic love: all these motivation systems are primarily orchestrated by dopamine pathways in the mammalian brain (see Fisher et al., 2006; Fisher, 2011). In fact, considerable behavioral data now suggest that human romantic love arose from mammalian antecedents (Fisher, 1998, 2004). Mammalian "courtship attraction" is focused on a *specific* individual, as well as associated with increased energy, obsessive following, affiliative gestures, possessive mate guarding, goal-oriented behaviors, and motivation to win this *preferred* mating partner (Fisher, 2004; Fisher et al., 2006; Fisher, 2011). These are central traits of human romantic love. However, in most mammalian species, courtship attraction is brief, lasting only minutes, hours, days, or weeks, while among humans, intense, early-stage romantic love can last twelve to eighteen months or much longer (Fisher, 2009; Acevedo et al., 2011, 2012; Fisher, 2016).

Perhaps the extended duration of human romantic love evolved in tandem with the evolution of human serial social monogamy to enable and sustain long-term social commitment for parenting (Fisher, 2011, 2016). In fact, romantic love has been called a commitment device (Buss, 1988; Frank, 1988; Fletcher et al., 2015; Sorokowski et al., 2017); and because relationship commitment has a direct, positive correlation with reproductive success in both sexes (Sorokowski et al., 2017), romantic love has also been referred to as a "survival mechanism" (Frascella et al., 2010; Fisher, 2016) that evolved to ensure one's genetic

viability in subsequent generations (Fisher, 2016).

Biopsychological Traits Associated with Mate Choice

But what activates this brain circuitry of romantic passion? What traits do human display choosers choose? Scientists have discussed a host of bodily traits that most likely evolved by mate choice in the EEA, including aspects of height, facial averageness, bilateral symmetry, scent, male jaw shape, female waist-to-hip ratio, resource control, and proneness to accidents and injury (Miller & Todd, 1998; Gallup & Frederick, 2010).

Researchers have likewise noted a host of psychological traits that men and women choose. Both sexes tend to choose individuals who share similar attitudes and values, a pattern known as homogamy; those from a similar socioeconomic and ethnic background; those with a similar level of education and intelligence; and those who share their religious views, political opinions, and social goals (see Fisher, 2011). Men and women gravitate to individuals with a similar sense of humor and social and communication skills. One's parents and childhood experiences play roles in mate choice, and individuals tend to choose a partner who reflects the values, interests, ideals, and goals of their friends during their formative years (see Fisher, 2011). Timing plays a role, as does proximity, and the major histocompatibility complex (MHC) component of the immune system appears to play a role in mate choice (Havlíček & Roberts, 2009).

Miller (2000) has proposed that humans have evolved a host of other behavioral and cognitive traits via mate choice. Among them are our increased human linguistic skills and musical abilities; our drive to create visual arts, stories, myths, comedies, and dramas; our agility at all kinds of sports; our intense curiosity; our ability to solve complex math problems; our moral virtue; our religious fervor; our impulse for charitable giving; our political convictions; our sense of humor; and our courage, pugnacity, perseverance, and kindness (Miller & Todd, 1998; Miller, 2000). Miller concluded that "the mind evolved by moonlight" (Miller, 2000, p. 7).

Four Neural Systems That Play a Role in Human Mate Choice

Fisher has proposed that four primary neural systems also play a role in human mate choice—the dopamine, serotonin, testosterone, and estrogen systems (Fisher, 2009, 2011, 2012; Brown et al., 2013; Fisher et al., 2015;

Fisher, 2016). Each of these four neural systems is associated with a distinct *constellation* or *suite* of related biobehavioral traits, known as temperament dimensions or behavior syndromes (Fisher, 2009, 2011, 2012; Brown et al., 2013; Fisher et al., 2015; Fisher, 2016).

The suite of biologically based traits associated with the dopamine system (DA) include exploratory behavior, novelty, thrill, experience and adventure seeking, boredom susceptibility and disinhibition, mania and hypersocial behavior, enthusiasm, energy, stamina, motivation and achievement striving, abstract intellectual exploration, cognitive flexibility, curiosity, idea generation, verbal and nonlinguistic creativity, low anxiety, and poor introspection (see Fisher, 2009, 2011; Brown et al., 2013; Fisher et al., 2015). This dopamine-linked behavior syndrome had been named the curious/energetic temperament dimension (Fisher, 2009, 2011, 2012; Brown et al., 2013; Fisher et al., 2015; Fisher et al., 2016).

The suite of biologically based traits associated with the serotonin system (5-HT) include adherence to social norms (conventionalism), self-control and self-regulation, sociability, harm avoidance, precision, interest in details, conscientiousness, orderliness, sustained attention, concrete thinking, managerial skills (cooperation, reduced commands, and reduced autonomous problem-solving), figural and numeric creativity, and self-transcendence or religiosity (see Fisher, 2009, 2011; Brown et al., 2013; Fisher et al., 2015). This serotonin-linked behavior syndrome has been named the cautious/social norm compliant temperament dimension (Fisher, 2009, 2011, 2012; Brown et al., 2013; Fisher et al., 2015; Fisher, 2016).

The suite of biologically based traits associated with prenatal testosterone priming include enhanced visual–spatial perception, mathematical skills, musical aptitude, aggressiveness, and compromised verbal fluency. Endogenous testosterone is also associated with enhanced attention to detail, focused attention, diminished emotion recognition, eye contact and social sensitivity, and reduced empathy. Characteristics correlated with activational testosterone (postnatal exposure) include enhanced self-assurance, candid and assertive communication, sensitivity to social dominance, drive for rank, and heightened sex drive (see Fisher, 2009, 2011; Brown et al., 2013; Fisher et al., 2015). This testosterone-linked behavior syndrome has been named the analytical/tough-minded temperament dimension (Fisher, 2009, 2011, 2012; Fisher et al., 2015; Fisher, 2016).

The suite of biologically based traits associated with prenatal estrogen priming include contextual thinking, linguistic skills, agreeableness, cooperation, theory of mind (i.e., intuition), empathy, and nurturing. In addition, activational

estrogen (postnatal exposure to estrogen) is positively correlated with generosity and trust, agreeableness, the drive to make social attachments, and heightened memory for emotional experiences. Similarly, oxytocin (secondarily associated with the estrogen system) is correlated with prosocial behavior, including trust, prosody, introspection, and perspective-taking (see Fisher, 2009, 2011; Brown et al., 2013; Fisher et al., 2015). This estrogen-linked behavior syndrome has been named the prosocial/empathetic temperament dimension (Fisher, 2009, 2011, 2012; Brown et al., 2013; Fisher et al., 2015; Fisher, 2016).

The Fisher Temperament Inventory

To study the possible role of these four broad temperament dimensions (or behavior syndromes) in human mate choice, a questionnaire was designed to measure the degree to which an individual expressed the traits associated with each of these four brain systems (Fisher, 2009). Reliability was obtained in a US sample of 39,913 anonymous men and women, using factor analyses and an Eigen analysis (Fisher et al., 2015). The final assessment measure was named the Fisher Temperament Inventory (FTI).

The FTI was also administered to subscribers of an international dating site (Match.com) in thirty-nine other countries, and reliability was confirmed among 15,000 individuals in six of these countries: Germany, France, Spain, Australia, Japan and Sweden (Fisher et al., 2015).

The FTI was also correlated with the NEO-FFI (or Big Five), a standard psychological measure, as an additional reliability index (Fisher et al., 2015).

Last, the FTI was administered to participants in two functional magnetic resonance imaging studies (fMRI) to measure the degree to which this psychological measure correlated with these four brain systems (Brown et al., 2013). Results indicated that those individuals who scored higher on the FTI scale measuring traits linked with the dopamine system also expressed more activity in primary dopamine pathways; those who scored higher on the FTI scale measuring traits linked with the serotonin system expressed more activity in a brain region associated with social norm conformity, a core trait of the serotonin system; those who scored higher on the FTI scale measuring the traits linked with the testosterone system also expressed more activity in neural regions built by fetal testosterone and regions associated with activational testosterone; and those who scored higher on the FTI scale measuring traits linked with the estrogen system also expressed more activity in neural regions associated with both organizational and activational estrogens. These results in two independent fMRI studies show that FTI scores on all four temperament

dimensions were directly correlated with appropriate and predicted brain regions and brain activity; thus correlational validity was established (Brown et al., 2013).

These above findings suggest that these four temperament dimensions constitute *foundational* mechanisms in personality structure (Fisher, 2009; Brown et al., 2013; Fisher et al., 2015).

The FTI was then employed to investigate *initial* mate preference in a random sample of anonymous participants on the online dating website, Chemistry.com (a member of Match Group Inc.). The sample consisted of 28,128 heterosexual adults (17,776 men, 10,352 women) who had just met a potential partner for the first time and given a positive rating of this partner after returning from this first date. First dates were studied because they were most likely to represent initial chemical attraction—a preference least likely to be contaminated by or facultatively adjusting to cultural factors and thus more likely to indicate preferences based on an evolved behavioral adaptation.

The Role of Four Temperament Dimensions in Mate Choice

Those men and women who expressed a disproportionately greater number of the traits associated with the dopamine system (the curious/energetic temperament dimension) initially preferred partners who also displayed a disproportionately large number of these dopamine-related traits (see fig. 31.1). Supporting this result, previous studies indicate that individuals with significant dopamine expression also tend to marry one another (Zuckerman, 1994). This dopamine-measuring temperament dimension of the FTI also correlated positively with the NEO-FFI domain for openness to experience (Fisher et al., 2015); and spouses who shared openness to experience were more satisfied with their marriage (Watson & Humrichouse, 2006); women whose husbands scored high on sensation seeking, a primary trait of the dopamine system, were more satisfied with their marriage (Charania, 2007), and wives' openness to experience was associated with the marital satisfaction of both husbands and wives (Donnellan et al., 2004; Claxton et al., 2012). These data are further evidence that the dopamine system plays a role in mate choic; specifically, those who disproportionately express these dopamine-liked traits initially prefer one another.

Those who expressed more of the traits linked with the serotonin system (the cautious/social norm compliant temperament dimension) tended to prefer partners who also displayed a disproportionately large number of these serotonin-related traits (see fig. 31.1). Supporting this result, previous studies

indicate that those who are cautious, a core trait of the serotonin system, disproportionately tend to marry one another (Zuckerman, 1994). Moreover, scores on the serotonin-linked scale of the FTI had a positive correlation with the Conscientiousness Scale of the NEO-FFI scale (Fisher et al., 2015); and individuals who score high on the NEO-FFI scale measuring conscientiousness tend to prefer and select one another (Little et al., 2006; Gyuris et al., 2010), further evidence that the serotonin system plays a role in mate choice; specifically, those who disproportionately express these related traits initially prefer one another.

Those men and women who expressed more of the traits linked with the testosterone system (the analytical/tough-minded temperament dimension) tended to prefer partners who displayed a disproportionately large number of traits in a different but complementary trait constellation, that linked with the estrogen system (see fig. 31.1). Supporting this result, previous studies indicate that high-testosterone men gravitate to high-estrogen women (Jones, 1995), further evidence that the testosterone system plays a role in mate choice; specifically, those who disproportionately express these testosterone-related traits initially seek their opposite.

Last, those who disproportionately expressed the traits in the estrogen system (the prosocial/empathetic temperament dimension) tended to prefer partners who displayed a lot of traits linked with the testosterone system (see fig. 31.1). Supporting this result, previous studies indicate that very feminine, high-estrogen women tend to form partnerships with very masculine, high-testosterone men (Feinberg et al., 2005), further evidence that the estrogen system plays a role in mate choice; specifically, those who disproportionately express these estrogen-related traits initially seek their opposite.

FTI Mate Preferences (*N* = 28,128)

		Female			
		Like Attracts		Opposites Attract	
		Dopamine	Serotonin	Testosterone	Estrogen
Male	Dopamine	117%	100%	93%	98%
	Serotonin	97%	111%	93%	91%
	Testosterone	99%	92%	100%	112%
	Estrogen	98%	93%	114%	99%

Figure 33.1 FTI mate preferences

Three Neural Patterns of Mate Choice

Three patterns of mate choice have emerged from the above data that may have evolved in the EEA, each for a different evolutionary purpose (Fisher, 2016).

1. Mate preference between individuals predominantly expressing the traits associated with the testosterone system and those predominantly expressing the traits of the estrogen system may have evolved to pool suites of *complementary* traits of temperament, a likely adaptive mechanism for competent parenting.
2. Mate preference between those expressive of the traits linked with the serotonin system may have evolved to capitalize on a suite of *similar* (and likely adaptive) parenting skills, including adherence to social norms, self-control, sociability, harm avoidance, conscientiousness, cooperation, and managerial skills. Other data suggest that marital partners who are *similar* in an array of personality traits are more satisfied with their marital partner, remain wedded longer, and bring up more children than those with fewer homogamous personality traits (Gyuris et al., 2010), data also suggesting that this preference for similarity is conducive to competent parenting.
3. It is more difficult to hypothesize the merits of mate preference by men and women who predominantly express the suite of traits linked with the dopamine system. Both partners are likely to seek novelty, thrills, and adventure, as well as being prone to boredom, disinhibition, mania, and lack of introspection—traits likely to contribute to an *unstable* long-term parenting partnership. But perhaps the potential instability of these partnerships had a genetic payoff in the EEA—leading to more extra-pair copulations and serial partnerships likely to produce more genetic variety in their lineages.

Data on 13,224 gay men and lesbian women, collected via Match.com in a national sample of singles (unpublished data), show some similar patterns of mate choice. Curious/energetic individuals (dopamine-linked) foremost chose to meet others like themselves. Cautious/social norm compliant individuals (serotonin linked) also preferred individuals similar to themselves in this temperament dimension. These data are similar to the data on Fisher's heterosexual population.

Unlike heterosexuals, however, those of the analytical/tough-minded temperament dimension (testosterone-linked) chose to meet others similar to themselves rather than those exhibiting many traits linked with estrogen, those of their opposite. And those of the prosocial/empathetic temperament dimension (estrogen-linked) also preferred those of the same biological profile, rather than their opposite. These data suggest that the heterosexual pattern of preference *complementarity* is a specific aspect of mate choice that evolved in the EEA for parenting, perhaps in tandem with the evolution of serial social monogamy (Fisher, 2009, 2011, 2016).

Mate Choice in the Digital Age: The *Singles in America* Study

Between 2010 and 2021, Fisher and Garcia examined mate choice among 55,000+ contemporary singles, in collaboration with the online relationship company Match.com; 5,000+ single adults were studied annually. In these studies, referred to as the *Singles in America* (SIA) data set, we used a demographically representative opt-in panel sample of single adults, based on national demographic distributions reported in the US census. Participants were all single at the time of survey. Some were casually dating; some were never married; some were divorced, separated, or widowed; all were between ages eighteen and seventy-plus; of all major sexual orientations; and from every major ethnic group and every region of the country. No members of the Match.com dating site or of any other site in the Match Group were polled or knowingly included. We used a third-party data collection company. This data set (unpublished) suggests several more biobehavioral and cognitive traits associated with mate choice that may have evolved in the EEA.

Physical Attraction as an Evolved Mechanism of Mate Choice

Men and women differed (respectively) in the degree to which they regarded it as "desirable" or "essential" that their potential partner be good-looking (92% M vs. 84% W; d = 0.39) and have a slender body (80% M vs. 58% W; d = 0.53). This predominantly male preference may have evolved in the EEA because being good-looking is a signal of parasite and disease resistance, health, and well-balanced hormone activities—important aspects of female fertility (see Buss, 1989; Miller & Todd, 1998; Miller, 2000).

Men and women (respectively) also differed in their preference for a financially stable partner, as first established in Buss (1989). Our data included someone with a steady income (74% M vs. 97% W; d = 1.17), someone who made/will make a lot of money (47% M vs. 69% W; d = 0.49), someone who made at least as much money as themselves (24% M vs. 46% W; d = 0.60), and someone who has a successful career (33%M vs. 61% W; d = 0.57). Women sought these qualities more than men, preferences likely to have evolved in the EEA because with the evolution of serial, social pair-bonding (Fisher, 2011, 2016), it would have been adaptive for ancestral females to prefer a partner who was a good provider. Supporting this hypothesis are the data that men cater to these female preferences: men lie about their finances (29 percent) and career success (32 percent).

These above data support extensive research that heterosexual men are

predisposed to seek female partners who can bear them healthy offspring and heterosexual women are predisposed to seek male partners who can help to provide for these offspring—adaptive preferences that most likely evolved in the EEA.

The top three physical attributes that singles notice first in a potential partner are their teeth (76 percent), their grammar (83 percent), and their self-confidence (78 percent). These may be yet more evolved physical preferences because one's teeth signal good health and age, one's grammar advertises their background and level of education, and one's self-confidence indicates their psychological stability and perhaps also their social status. All are reliable indicators of reproductive quality that may have evolved.

Relationship Transparency as an Evolved Mechanism in Mate Choice

Today's display choosers seek psychological transparency in a potential partner: 77 percent of women and 53 percent of men would not date someone who is secretive with their texts; 69 percent of women and 47 percent of men would not date someone who answered their cell phone calls discreetly; and 74 percent of women and 48 percent men would not date someone who wouldn't let them use their cell phone. These large sex differences suggest that women are considerably more concerned about transparency than men, perhaps because women generally play a larger role in hands-on parenting and have thus evolved a somewhat greater predisposition to focus their courtship energy on more stable relationships. These sex differences also suggest that men are more likely to seek a short-term mating opportunity in which transparency is less important.

Some 60 percent of singles think it is rude to text during a date; and 43 percent of singles are turned off by someone who hides information from them on social media. Singles also regard it as rude (while on a date) to take one's phone to the bathroom or outside the venue or to answer their phone secretly and without explanation. Moreover, more than 90 percent of singles (including gays and lesbians) also seek a partner whom they can trust and confide in (98 percent), and 56 percent worry about whether they are assessing a potential partner accurately.

This preference for relationship transparency could have evolved because transparency generally signals commitment. And greater partnership commitment is correlated with more offspring (Sorokowski et al., 2017) and less divorce (Cherlin, 2010), phenomena associated with higher long-term

reproductive success.

Laughter and Humor as Evolved Mechanisms of Mate Choice

Some 96 percent of today's display choosers prefer a partner who makes them laugh, most likely also for evolved adaptive reasons. Laughter upregulates the dopamine system to generate optimism, energy, focus, and motivation. Laughter also boosts the immune system and the endorphins (associated with painrelief), elevates heart rate and blood circulation, builds muscle tone, reduces inflammation after injury, and stimulates brain growth. Moreover, laughter can diffuse arguments to alleviate relationship tension, as well as entertain in stressful situations. All these biobehavioral payoffs of laughter are likely to contribute to general health and longevity—important contributions to reproductive potential, parental competence, and overall survival, thus likely to have evolved in the EEA.

Interestingly, 85 percent of singles are particularly attracted to wit, as opposed to puns (60 percent), sarcasm (50 percent), dry humor (49 percent), sexual innuendos (39 percent), political humor (38 percent), self-deprecating humor (33 percent), offensive humor (17 percent), or bathroom jokes (6 percent). Wit may be a preferred trait because puns are unexpected linguistic juxtapositions which aren't funny to everyone, sarcasm and offensive humor can be taken as rude, dry humor can be hard to understand, sexual innuendos can appear sexually threatening or signal a short-term mating strategy, political humor can offend one's values, and self-deprecating humor can be mistaken for weakness. Moreover, wit is associated with creativity. And creativity has been linked with intelligence, energy, and resilience—traits that are likely to be adaptive for rearing young. Hence the preferences for laughter and wit are likely to have evolved in the EEA.

There is a gender difference in wit producers, however. When singles in the SIA data set were asked, "Have you ever fallen in love with someone because of their sense of humor?" 57 percent of women said "yes," as opposed to 40 percent of men. Thus, a man's sense of humor plays a larger role in female mate preference. So it is not surprising that men believe it is more important to be humorous than do women (men, 79 percent; women, 50 percent). Today male display producers with a sense of humor have an advantage in the mating market; hence sense of humor may have evolved as an adaptive courtship strategy.

Lying as an Adaptive Trait That Evolved via Mate Choice

Three forms of lying, known as "impression management," may have evolved in the EEA because each appears to have adaptive value today.

Women (consciously or unconsciously) lie about their weight (17 percent W vs. 10 percent M), most likely because overweight women have more problems with fertility. They are more likely to have trouble conceiving, to have a miscarriage, and to have chronic diseases. Hence in the EEA, it would have been adaptive for men to prefer women of normal weight, selecting for an evolved female strategy to lie when not of optimal weight. Men lie about their finances (29 percent) and their job (32 percent). These male mating strategies must have had mate value in the EEA because ancestral females most likely sought males who could help provide for their young, another predisposition that could have emerged with the evolution of serial social monogamy by 4.4 million years BP (Fisher, 1992, 2011, 2016).

Both sexes lie about orgasm: 37 percent of men have faked or pretended an orgasm and 41 percent of these men faked orgasm to show their partner that they loved them, whereas 72 percent of women have faked or pretended orgasm, and 39 percent also said they faked it to show their partner that they loved them. Faking orgasm is not taught by parents, friends, colleagues, books, or school systems. Instead, faking orgasm appears to be a courtship tactic—an adaptive courtship strategy that could have evolved among display producers of both sexes in the EEA to trigger and/or sustain a mating partnership.

The Role of Uncommitted Sex in Mate Choice

Some 63 percent of single men and 83 percent of single women would prefer a traditional romantic relationship to an uncommitted sexual event; 32 percent of singles agree that you have to be in love to have great sex (M = 28 percent, W = 36 percent), and 84 percent say sex is better when you're in love. Nevertheless, 77 percent of singles approve of premarital sex, 52 percent have had a one-night stand (58 percent men; 45 percent women), and 55 percent have had a friends-with-benefits relationship.

Because casual, uncommitted sex can lead to disease, unwanted pregnancy, and/or social ostracism, it is parsimonious to suggest that singles engage in uncommitted sex because they accrue some reproductive payoffs from it. They do. Our SIA data indicate that 35 percent of singles have had a one-night stand turn into a long-term partnership, and 45 percent have had a friends-with-benefits relationship turn into a committed relationship. Other research supports

this finding, reporting that 50 percent of women and 52 percent of men have had casual sex turn into a committed partnership (Garcia & Reiber, 2008). Interestingly, men were three times more likely than women to say that a one-night stand is useful because it can lead to a relationship; men were also two times more likely to say that they have one-night stands to find a long-term partner.

This tendency to engage in uncommitted sex may have evolved. With uncommitted sex, the *display producer* is able to signal that they can attend to their partner's sexual needs, and uncommitted sex enables the display chooser to assess the physical and mental health of the display producer. In fact, 28 percent of millennials report that they have uncommitted sex to see if they love someone. Today, singles appear to use uncommitted sex as a form of interview as they assess potential mating and parenting partners.

Some 33 percent of single men and 32 percent of single women have also sent a sexy photo to a potential partner, and 58 percent of men and 41 percent of women have received one—despite the fact that 75 percent of singles believe that "sexting" can jeopardize their reputation and 72 percent believe it can hurt their career. Sending sexy photos, despite the consequences, suggests that display producers regard "sexting" as a selling strategy, and display choosers use these photos to assess the physical attributes of these display producers. Sexy photos were not available in the EEA. But our forebears may have advertised their bodies through dance and athletic competitions instead, selecting for the impetus of today's display producers to send sexy photos and display choosers to assess the qualities of these display producers via these displays. Both propensities are likely evolutionary strategies associated with mate choice.

Age and Mate Choice

Our SIA data suggest that single women approaching menopause alter their behavior, becoming less likely to establish relationship exclusivity prior to sexual activity with a new partner. Moreover, after the typical age of menopausal onset, women return to former (elevated) levels of commitment choosiness. Men exhibit similar, though attenuated, changes in midlife (Cohen et al., 2019). These changes in mating strategies would have been adaptive in the EEA.

With advancing age, display choosers alter their mating strategies in other ways as well (Fisher, 2016). When singles were asked, "How likely are you to make a committed relationship with someone who offers everything you are looking for in a relationship but with whom you are not in love?" the older one gets, the more discriminating they become: Of those ages twenty to twenty-nine

and thirty to thirty-nine, 30 percent were “very likely” or “somewhat likely” to make a commitment even when not in love. But after reproductive years are largely over, singles become less and less likely to make a commitment without being in love (ages forty to forty-nine: 27 percent; ages fifty to fifty-nine: 26 percent; ages sixty +: 23 percent). The older one gets, the less likely they are to compromise and make a commitment to someone with whom they are not in love.

The same trend emerged when singles were asked, “How likely are you to make a committed relationship with someone who offers everything you are looking for in a relationship, but whom you don’t find sexually attractive?” Of those ages twenty to twenty-nine, 31 percent were “very likely” or “somewhat likely” to make this compromise; and among those ages thirty to thirty-nine, 28 percent were “very likely” or “somewhat likely.” But after reproductive years are largely over, singles become less and less likely to make a commitment to someone without sexual attraction (forty to forty-nine: 22 percent; fifty to fifty-nine: 23 percent).

Perhaps those of reproductive age are the most likely to compromise because the young are obliged to choose a partner with whom they can reproduce. The predisposition to compromise *during reproductive years* may be another aspect of mate choice that evolved in the EEA (Fisher, 2016).

Deal-Breakers in Mate Choice

Mate preference research has largely focused on traits people desire in partners (deal-makers) rather than the traits they avoid (deal-breakers) (Jonason et al., 2015). Nevertheless, today’s display choosers have traits they choose to avoid.

When display choosers in our SIA samples considered a committed relationship (Jonason et al., 2015), their top deal-breakers included disheveled or unclean appearance (67 percent); laziness (66 percent); being too emotionally needy (63 percent); lacking a sense of humor (54 percent); living more than three hours away (49 percent); bad sex (47 percent); lacking self-confidence (40 percent); watching too much TV or playing too many video games (33 percent); having low sex drive (33 percent); talking too much (23 percent); and airing emotional drama in social media posts (61 percent). Almost all of the above deal-breaker traits are associated with either mental instability or lack of sincere interest in the partnership. So the disposition to avoid these traits may have evolved in the EEA as more adaptive mechanisms.

Another case of mating aversion in the modern digital world involves sex

with a robot. Although 31 percent of men and 15 percent of women would have sex with a robot, nearly half of singles would consider it cheating if their partner had sex with a robot (39 percent of men; 56 percent of women). Perhaps this sex difference stems from the fact that men can't be cuckolded if a female partner has sex with a robot; while male sex with a robot may threaten a woman with the potential withdrawal of her mate's attention and emotional support, both likely to be critical to the parenting of her young in the EEA. Regardless, display choosers of both sexes appear to dislike anything they associate with adultery, a likely predisposition that evolved in prehistory because relationship infidelity can lead to genetic cuckoldry for males and a loss of protection and provisioning for females—destabilizing the pair-bond and leading to reproductive failure.

Today's display producers also believe that signals of poor health and mental, financial, and career instability are deal-breakers in the mating market, so they strive to be prepared. Some 40 percent feel they need self-acceptance (a signal of mental stability) before they pursue a relationship; 23 percent feel they need to reach a certain point in their career; 20 percent feel they need to reach a certain income level; 29 percent say their financial situation is a barrier to pursuing love; 16 percent say they must first pay off debt; and 28 percent feel they must first lose weight. Singles appear to believe that these issues jeopardize their viability in the mating market.

Altering Patterns of Mate Choice in the Digital Age

The current proliferation of digitally mediated introducing platforms also affects mate choice. In the SIA data set, 40 percent of American singles met their last first date on the internet, whereas only 25 percent met through a friend and 6 percent met in a bar/restaurant. Moreover, some 51 percent of singles research a date on Facebook, and 34 percent use Google to investigate a potential partner. On these venues, one cannot touch, see, smell, or contextualize a potential mating partner. So alternative cues to health, interests, and personality are becoming more important in triggering mate preference, particularly those traits most visible in a photograph (Fisher & Garcia, 2019).

One's written descriptions of themselves on dating sites/apps are also becoming important. With no knowledge of a potential partner's background, family, or social networks, today 57 percent of single men and 61 percent of single women report that they carefully evaluate a profile, and only 30 percent report that they swipe quickly through these profiles.

An evolutionary strategy of female display choosers is also emerging. Today, 75 percent of men say they would be comfortable if a woman was the first to say

hello on a dating app/site, yet only 19 percent of women regularly take this lead; 90 percent of men are happy to have a woman ask them for their phone number, yet only 14 percent of women often do; 90 percent of men would be happy if a woman initiated the first kiss, yet only 15 percent of women often do; 84 percent would be pleased if a woman initiates sex for the first time, yet only 12 percent do; and 68 percent of men in every major ethnic group would be "very comfortable" or "somewhat comfortable" if a female partner proposed marriage.

Perhaps women's wish to remain the display choosers is driven by evolutionary requirements. Women expend more metabolic energy and time in reproduction—due to months of pregnancy, the energy expenditure and danger of parturition, and women's primary role in infant care cross-culturally. So it is to women's reproductive advantage to remain the primary display choosers, thus able to assess potential partners and select those of greater mate value.

The 2020 coronavirus pandemic is also altering patterns of mate choice, due to the rise of video chatting (Fisher, 2020). Prior to the US pandemic beginning in February/early March 2020, only 6 percent of Match.com members used video chatting *before* meeting in person, but by mid-March, 69 percent of singles in our SIA sample were open to video chatting before meeting on a first date, and by August, 19 percent had engaged in video chatting. In our 2021 SIA study, 27% of singles had used video chatting; and 51 percent of Gen Z and 46% of Millennials has used video chatting prior to meeting in person.

This new stage in the courtship process is enabling display producers to advertise more details of their mate value (including showing their home, pets, companions, and the trappings of their lifestyle and interests) before meeting. Video chatting is also enabling display choosers to assess these accoutrements before meeting in person. In fact, as of August 2020, 68 percent had used video to vet a potential partner, 56 percent had felt some romantic chemistry during a video chat, and 50 percent had fallen in love.

The Fluctuating Frequency of Mate Choice

The primary human reproductive strategy in almost every society on record is pair-bonding, a reproductive strategy that could have evolved some 4.4 million years BP (Fisher, 1992, 2004, 2011; Gray & Garcia, 2013; Fisher, 2016) to ensure the survival of highly altricial young that required many years of parenting. Thus, across prehistory (and today), people of reproductive age have been obliged to invest considerable time, metabolic energy, and resources to assess and choose effective *long-term* parenting partners. Moreover, due to the cross-cultural high divorce rate (Fisher, 1992, 2016), many men and women are

obliged to return to the mating market and renew the process of mate choice periodically throughout the life course. Adultery is common cross-culturally as well (Fisher, 1992; Tsapelas et al., 2010; Fisher, 2016), also predisposing men and women to engage in mate assessment and mate choice periodically across their lives—sustaining high levels of mate choice.

However, countering this evolutionary trend toward lifelong courtship display and mate choice is an emerging social trend known as "slow love" (Fisher, 2016; Fisher & Garcia, 2019). Men and women are now marrying (on average) in their late twenties rather than in their early twenties. And data on eighty societies collected between 1947 and 2011 by the Demographic Yearbooks of the United Nations, as well as several ethnographic studies, indicate that the later you marry, the more likely you are to remain married (Fisher, 1992, 2016).

Supporting these data, a study of more than three thousand married Americans indicates that couples who dated for one to two years (compared to those who dated less than a year prior to wedding) were 20 percent less likely to get a divorce, and couples who dated for three years or longer were 39 percent less likely to part (Francis-Tan & Mialon, 2015). So, to some degree, the extension of the precommitment stage of courtship and subsequent later marriage may reduce the frequency of lifelong courtship display and mate choice.

Conclusion

Fisher has proposed that the neural system associated with feelings of intense romantic love evolved in tandem with human mate choice to provide the focus, motivation, and energy to pursue preferred mating partners. This brain system provides only general motivation, however. Specific mate preferences appear to be guided (in part) by a different set of neural systems: the dopamine, serotonin, testosterone, and estrogen systems.

A literature review indicates that each of these four neural systems is associated with a distinct *constellation* of related biobehavioral traits. So the *Fisher Temperament Inventory* was constructed to measure the degree to which participants express the traits associated with each of these four primary brain systems. This personality measure was administered to fifteen million + single men and women in forty countries and validated in a population of 39,913 Americans using factor analyses, an Eigen-value analysis, two neuroimaging (fMRI) studies, and correlations with a standard personality measure, the Big Five. Then, using a population of 28,128 single Americans, it was established that those who primarily express the traits in each of these four basic brain

systems expressed initial romantic attraction in specific patterns.

Those individuals particularly expressive of the traits associated with the dopamine system, including risk taking, novelty seeking, curiosity, creativity, and mental flexibility tend to initially gravitate to individuals who share these traits. Those individuals primarily expressive of the traits biologically linked with the serotonin system in the brain, including conventionality, harm avoidance, concrete thinking, and adherence to rules and schedules, also disproportionally express an initial attraction to those with similar traits. Those individuals particularly expressive of several traits in the testosterone system, including assertiveness, tough-mindedness, skepticism, fairness and mathematical/spatial aptitudes, initially gravitate to those expressive of the traits linked with the estrogen system. And those individuals primarily expressive of several traits in the estrogen system, including contextual thinking, linguistic skills, and prosocial skills including empathy and nurturing, are disproportionately initially attracted to those expressive of traits in the testosterone system.

Fisher has proposed that these biologically based patterns of mate choice may have served different adaptive purposes in the EEA: (1) the high-testosterone/high-estrogen partnerships may have served to pool *complementary* traits useful for parenting; (2) high-serotonin partners may have benefited from their *shared* parenting traits; and (3) high-dopamine partners (who express several destabilizing traits) may have disproportionately practiced *serial* pair-bonding in the EEA, thereby producing more genetic variety in their lineages.

A host of psychological traits also play a role in mate choice. To further this research, we used a sample of 55,000 single adult Americans to explore current trends in mate choice, specifically those preferences that are likely to have evolved in the EEA via mate choice.

We found that men are considerably more likely than women to seek a female partner who is good-looking and has a slender body, while women are considerably more likely than men to prefer a financially stable male partner. The top three physical attributes that single men and women notice first in a potential partner are their teeth, their grammar, and their self-confidence—traits respectively likely to express one’s health and age, one’s background and level of education, and one’s self-confidence and thus psychological stability. Today’s singles also prefer partners who express relationship transparency. They gravitate to humorous individuals. Courting women lie about their weight, courting men lie about their financial stability, and both sexes fake orgasm to please their partner. Last, middle-aged singles change their courtship strategies to secure a preferred partner. All these courtship strategies are likely to be

adaptive mechanisms that evolved via mate choice in the EEA.

Today's display choosers also have a host of traits they do *not* prefer in a mate. These deal-breakers include disheveled or unclean appearance; being too emotionally needy; lacking self-confidence; watching too much TV or playing too many video games; airing emotional drama in social media posts; lacking a sense of humor; engaging in sex with a robot; and bad sex. These are more courtship strategies likely to be adaptive preferences that evolved in the EEA.

Due to the human inclination for serial monogamy (divorce, repartnering/remarriage) and extra-pair copulation (adultery), many men and women return to the mating market periodically across their lives. Nevertheless, countering these predispositions, men and women in industrialized societies are currently marrying later—regularly in their late twenties rather than in their early twenties. And cross-culturally, the longer one courts and the later one marries, the more likely they are to remain married. This current trend, "slow love," is likely to reduce the incidence of mate choice across the life course, potentially contributing to a few decades of relative family stability.

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CHAPTER
34

Popular Culture and Human Mating: Artifacts of Desire

Catherine A. Salmon and Rebecca L. Burch

Abstract

The products of popular culture, including pornography and romance, can be viewed as artifacts of human sexual psychology. In other words, popular culture can be examined as data in testing theories about human psychological adaptations in the same way as archaeological artifacts can be used by anthropologists to test hypotheses about human evolution. From a methodological standpoint, there are clear benefits to this approach (as opposed to surveys, for example) in that such unobtrusive measures do not require the cooperation of participants, or their honesty or self-awareness, and it does not influence the participant response. Additionally, media outlets can provide much larger samples reporting actual use. In this chapter, we will examine how the products of popular culture illuminate our understanding of male and female sexual desires with a particular emphasis on the appeal of mythology, pornography, and various forms of romance (from romance novels to Bollywood, erotica, and slash). Not only are there differences and overlap in mass media marketed to men and women but also in the media they create themselves. These differences not only inform researchers regarding what men and women desire, but also where more research needs to be conducted.

Key Words: pop culture, unobtrusive measures, sexual psychology, sex differences, romance, pornography, Bollywood

Evolutionary insight via popular culture

You might be asking yourself, why is there a chapter on popular culture and pornography in a handbook of human mating? The short answer is that the products of popular culture can be viewed as artifacts of human sexual psychology, providing unobtrusive insight into the nature of human mating. Popular culture can be used as data in testing theories about human mating adaptations in much the same way as archaeological artifacts can be used by anthropologists to test hypotheses about human evolution. For the purpose of this chapter, popular culture is defined as "culture based on the tastes of ordinary people rather than the elite class" (Salmon, 2018, 47). This definition includes both cultural activities and commercial products that have mass appeal. Some of the most popular genres of pop culture involve storytelling. Even though such genres may be evolutionary novel, their content is not. Their stories focus on the problems humans have always faced, ones of survival, competition, mating, parenting, and social living. Their essential storylines draw in their readers and watchers because they tap into the evolved psychological mechanisms we have for managing these problems. Although some or all of these problems may be explored in many types of popular culture (Salmon, 2016; Salmon & Burch, 2020), our attention here will focus on how the problems of human mating are explored in mythology, comic books, Indian (specifically Hindi) cinema, romance, pornography, and manga.

Adaptations and Sexual Desire

The nature of sexual reproduction over the course of human evolution guarantees that ancestral men and women faced different reproductive opportunities and constraints, and, as a result, selection has produced different psychological adaptations to solve those problems. Choosing the best possible mate was an adaptive problem faced by men and women. Potential mates vary in mate value or what benefits they provide. What constitutes mate value is different for men and women. For example, superior physical strength and hunting skills would allow men to contribute more resources to their families in the ancestral environment and would be considered higher mate value in comparison to weaker men who were poor food providers. Similarly, an eighteen-year-old woman, on average, would have greater mate value than a fifty-year-old woman, because the younger woman has many child-producing years ahead of her while the older woman has none. The result is psychological adaptations, shaped by natural or sexual selection, specialized to process information about mate quality. These adaptations are somewhat different for males and females because the specific information relevant to successful mate

choice is not identical for males and females.

Men's mate preferences are heavily influenced by cues of fertility and reproductive value (Confer et al., 2010; Symons, 1995) such as body shape, including waist-to-hip ratio and body mass index (Lassek & Gaulin, 2019; Platek & Singh, 2010), as well as hair and skin quality (Hinsz et al., 2001; Sugiyama, 2005). When men engage in long-term mating, other traits also come into play, such as indicators of sexual fidelity (Buss & Schmitt, 1993), so that they will not be faced with the problems of paternity uncertainty. This is illustrated well in Hindi romance films, as long-term (lifetime) mates are the typical goal and female chastity (an indicator of long-term faithfulness) is a prominent trope. Pornography, whether online or off, is focused on short-term mating, meaning that cues related to fertility and indicators of sexual promiscuity are ubiquitous. Women signaling promiscuity is important in this short-term context because it suggests that men do not have to invest a great deal to obtain sex with any specific woman. Men generally have a greater interest in short-term mating opportunities (Symons, 1979; Trivers, 1972) than women, and for it to be a successful strategy, there must be a variety of fertile convincible women available.

For ancestral women, finding a fertile man was not the adaptive problem. However, the greater minimal investment required by women (Trivers, 1972) in offspring means that she must be highly selective in her choice of long-term mate with regard to particular qualities. The mate that is providing his DNA must also be willing and capable of contributing the resources required to successfully raise offspring. The result is female mating adaptations that are sensitive to cues that a male is capable of providing economic resources, or has good prospects for doing so in the future (Buss et al., 2001). Women also exhibit preferences for men of high status (Li, 2007), typically associated with access to resources, as well as men who are dependable (Buss et al., 1990) and demonstrate a willingness to invest in children (Roney et al., 2006). Physical height and strength are also seen as desirable (Courtiol et al., 2010; Hughes & Gallup, 2003), as well as indicators of genetic quality including facial symmetry and masculinity (Thornhill & Gangestad, 2006).

Although women have evolved a general preference for long-term mating strategies, they incorporate short-term mating strategies as well (Buss & Schmitt, 1993), including strategies related to infidelity (Gildersleeve et al., 2014). Studies of heterosexual, naturally cycling, college women's self-reported mate preferences show shifts around ovulation (when they might be considering a short-term liaison) emphasizing good genes cues, symmetry, and high masculinity (Gangestad, et al., 2005; Pillsworth & Haselton, 2006). Under some

circumstances, short-term preferences for women seem to place more value on physical attractiveness than their long-term preferences which are more likely to take into account a future possible dad role. However, the mate-switching hypothesis has challenged the importance of the infidelity approach, suggesting that short-term mating may occur for long-term goals when costly relationships are being abandoned in the pursuit of a better quality mate (Buss et al., 2017). So although "good genes" are one possible motive for female short-term mating, a number of recent studies have provided support for the mate-switching hypothesis (Boutwell et al., 2015; Conroy-Beam et al., 2016; Greiling & Buss, 2000; Lewis et al., 2011; Perilloux & Buss, 2008). Here the factors influencing short-term mating include mate insurance, developing possible backup mates, and assessing the options for switching mates, particularly 'trading up', so to speak.

Mythology

Some examples of modern media may come to mind when reading these various preferences; romantic comedies, romance novels, erotica, and so on. However, these preferences are not new, and neither are the stories that illustrate them. Storytelling is a human universal, has existed for millennia, and is practiced throughout traditional societies (Gottschall, 2012). As Gottschall states (particularly of religious texts), it is "a collection of intense narratives about the biggest stuff in human life" (p. 117). As such, they are unobtrusive measures of human behavior throughout the history of the species. Dowden (1992) suggests that Greek myths are "not to tell history, only to masquerade as history. Not just to entertain: they have too much cultural significance for that" (p. 22). We argue that this significance isn't just cultural but evolutionary, with each area's mythology (Greek, Roman, Norse, Indian, African, etc.) illustrating human nature in both evoked culture and metaculture (see Tooby & Cosmides, 1992), which have been influenced by evolution. We can examine myths as stories that reflect the preferences and priorities of human beings as a species, with small variations reflecting their culture of origin.

Greek mythology has illustrated male and female preferences for millennia, and scholars have noticed. What does ancient mythology tell us about sexuality? Primarily written by men (given the gender dynamics and power structure at the time), these stories depict male preferences. It is not surprising that in myth, powerful men use their power to seek out multiple sexual opportunities in both long-term and short-term pairings. They typically seek out virginal women and father many children. Zeus, for example, is depicted as extremely promiscuous,

using a variety of tactics to seduce or coerce virginal women (nymphs, mortals, and gods) into sex (Chrystal, 2016). In an entertaining turn of phrase, Chrystal describes this as “Zeus played the Olympian field with unbridled and endless gusto” (p. 25). It is argued that it is impossible to list all of his children and the lowest estimate of lovers would be over fifty. Zeus is not the only male character in Greek mythology to behave thusly. Both god and mortal men had tryst after tryst, some by seduction, some by trickery, and some by force. Poseidon for example, had over forty conquests, including turning into a horse to have sex with Demeter and raping Medusa. Female resistance to male advances was punished; Echo was ordered killed by Pan when she refused male advances and was torn to pieces. Women who gave in were not necessarily spared, either punished by their male partners or female rivals. Greek myths tell a similar tale of male mating psychology as that revealed by a variety of research methods (Buss & Schmitt, 1993; Symons, 1979).

Human women in Greek mythology were depicted as young, beautiful, virginal, chaste, and ashamed when duped into sex. Women (particularly goddess and nymph) were also portrayed as faithful wives, unattractive crones, and sexy sirens. Promiscuous women were often depicted as villains, befitting male mating preferences for faithful wives (Knoblauch, 2007). Hera was a particular trope; as Chrystal phrases it, the “disputatious and duplicitous schemer deploying sexual power” (p. 19). The stories of Aphrodite, the goddess of beauty and love, illustrate intrasexual competition, both male, with men competing and waging war for her affections, and female, with women jealous of the powers her beauty afforded her. Eris, the goddess of discord, sets off female competition by giving Athena, Hera, and Aphrodite one golden apple, inscribed with “for the fairest,” triggering the Trojan War.

Other epic origin stories of the gods repeat themes of males threatening or destroying their children while females try to protect and care for them, males going to war over power and sexual conquests, jealousy between siblings, and other evolutionarily relevant phenomena. Chrystal (2016) calls these gods “the embodiment of typical masculine and feminine sexual qualities” (p. 19) and the Greek myths are not alone. These qualities repeat themselves in stories of Jupiter in Roman mythology, the Norse gods Thor and Odin, the Hindu deities (e.g., Indra), and the Gods of other cultures. Any mythology can be studied extensively in evolutionary terms; mating preferences, power structures, social contracts, and family dynamics. In addition, the similarities between the story of Athena, Hera, Aphrodite, and the apple in the fairy tale of Snow White should not be lost on the reader. The themes, and sometimes specifics, of mythology are reiterated through fairy tales, epics, and other forms of storytelling.

The Mythological World of Comics

It is no surprise given the cultural obsession with these themes that various populations have created stories similar to ancient mythology. Some genres, like comic books, create gods and superhumans and, in some cases, use preexisting mythological gods as characters (several comic book worlds include the Greek gods and Marvel has Norse gods as major characters, for example) (Burch & Johnsen, 2020). Comic books contain all the same evolutionary themes: competing for resources, status, ingroup/outgroup and family dynamics, and of course, mating. Comic book characters have the same multiple partners, scandals, and indiscretions in addition to having the superhuman powers of the gods. One of the distinctive facets of comic books, however, is that the storytelling is far more visual, thereby providing readers with not only evolutionarily salient storylines but also visualizations. Comics and other graphic formats give us the opportunity not only to see what narratives are most popular but also what body types and artistic styles. Not only do comic books depict the "the embodiment of typical masculine and feminine sexual qualities," but they depict the embodiment of masculine and feminine sexual *bodies*. In fact, these drawings, in an attempt to exemplify male and female bodies, can become so exaggerated that they become hypersexual, supernormal stimuli.

Burch and Johnsen (2020) examined samples of up to 3,700 Marvel Comics characters. As Marvel has long catered to a male readership, Burch and Johnsen (2020) expected depictions reflecting male preferences; a wide range of shapes and sizes that male readers can identify with, with hero males displaying strong testosterone markers and sexy female characters with large breasts, small waists, and large hips, youth and fertility markers. They found that the average male bodies measured the 74.6 inches (189.5 cm) tall and 255.7 pounds (115.9 kg) according to Marvel-provided measurements. When measuring the bodily dimensions of these comic book bodies as depicted on the page, given a 34-inch (86.4 cm) waist, male hips were 37 inches (94 cm) and shoulders were an astounding 73.71 inches (187.2 cm). Comic book men had a shoulder-to-waist ratio and upper-body muscularity almost twice that of normal college men. This body shape is an extremely exaggerated "mesomorphic" body shape displaying testosterone markers and reflects the preference of this body shape in the predominant fan base, men and boys. Dibiase and Hjelle (1968) found that 100 percent of their male participants desired the mesomorphic body type and its display of testosterone, upper-body strength, and muscularity.

Female comic book characters were exaggerated as well, their bodies remarkably uniform—thin, yet very curvy. For example, almost a quarter of

comic book women possessed body mass indexes that were underweight, compared to only 3 percent of the US population. Comic book women were on average 68.0 inches (172.7 cm) tall, weighed 131.5 pounds (59.6 kg), and given a 24- inch (61 cm) waist, measured 36 inches (91.4 cm) at the chest and 40 inches (101.6 cm) at the hips (Burch & Johnsen, 2020). These dimensions gave the average comic book women a smaller waist-to-hip ratio than the most searched female porn stars on Pornhub.com. One might assume that these preferences are specific to this form of media, but Lassek and Gaulin (2016) compared a large sample of college women, a large sample of Playboy Playmates of the Month, and a large pool of imaginary women (e.g., cartoon, video game, and graphic novel characters) chosen as the "most attractive" by university students. They also found that waist size was a key determinant of female bodily attractiveness. Each of these industries (Playboy, video games, graphic novels) cater to a primarily male fan base. Given the very visual medium of comic books, human preferences are being displayed in the physical depiction of characters, not to mention the storylines. Overall, comic books are reflecting the preferences of their male audience, exaggerating that into impossible bodies. We have likened these depictions to supernormal stimuli, "visual cotton candy," providing instant gratification but not supplying any real substance.

Comic storylines are just as revealing regarding sexual preferences. Characters have multiple partners, marriages, affairs, and love triangles. One particular Marvel character, for example, Jean Grey, is perpetually vexed with choosing either her faithful and steady love, Scott Summers (Cyclops), or the fierce and intriguing Logan (Wolverine). One popular plotline is the kidnapping of a heroine by a villain, replete with bondage, brainwashing, and seduction, only to be rescued by the kind and faithful partner in the end. Both the love triangle and this "kidnapping" plot point to a well-researched female mating strategy—maintaining a long-term monogamous relationship while seeking out other virile males for brief relationships and the fathering of offspring (Benshoof & Thornhill, 1979; Gangestad et al., 2005; Pillsworth & Haselton, 2006). We also see these tropes in mythology, soap operas, and films.

Bollywood and Romance

Lest the reader think these forms of media reflect a primarily Western aesthetic, or that this is a specifically Western phenomenon, let's turn our gaze to the largest film industry in the world. The Indian film industry makes more films per year than any other (stephenfellows.com) and was second in box office tickets sold and third in revenue in 2019 (Statistica.com). Indian film can be

divided up by region and language, with the most prominent being the Hindi industry, centered in Mumbai (nee Bombay) and nicknamed “Bollywood.” It is important to note that Hindu mythology is rich in amazing stories of love, betrayal, jealousy, and punishment, and Hindi cinema dips into that well deep and often, in some cases reenacting the myths, in others creating thinly veiled modern versions.

In order to be successful, an Indian film must appeal to viewers who differ by language; gender, age, caste, religion, class, education, and urban/rural location (Srinivas, 2002). However, even in a country of a billion people, India is largely patriarchal, with men in positions of power in the family, the culture, and in media. Men are also the predominant consumers of film, with a movie going population that is 72 percent male and 39.7 percent in the twenty-five- to thirty-four-year age range (Statistica.com). Therefore, Indian film has a strong male bias, both in representation and in plot. In essence, the industry attempts to appeal to “everyone” with men at the forefront, and this includes male evolutionary preferences.

The Indian film industry has a profound effect on the culture, and vice versa. Ahmed (1992) condenses it into one sentence, “Political philosophies, social values, group behavior, speech and dress in society are reflected in the cinema and, like a true mirror, reflect back in society” (p. 289). He also states that the cinema is a legitimate metaphor for society and provides insights into societal priorities. You will notice above in Ahmed’s reflection of culture, he did not mention “sexuality” as such. This is because in 1992 (and well into the 2000s), sexuality, particularly female sexuality, was restricted in film and culture. Then how was sexuality depicted? Khan and Taylor (2018) rightly surmised that gender stereotypes in media are more frequent in cultures with less egalitarian norms, and the patriarchal culture prominent in India prefers tall, muscular, athletic, coordinated, romantically assertive, and exceedingly tough men and soft, curvy, demure, chaste, and passive women. Khan and Taylor (2018) examined a hundred commercial Hindi films (from 2003– 2004 and 2013 to 2014). All had central male characters, eleven had no central female characters. Central female characters were portrayed as patient, empathic, emotional, devoted, soft spoken, trusting, and family oriented. If that is not enough, Madaan et al. (2018) examined descriptions of four thousand films and found that men were portrayed as rich, wealthy, strong and successful, and women were portrayed as beautiful, attractive, lovely, and pretty. Males were generally introduced with a profession while females were either introduced using physical appearance or in relation to another (male) character, like a daughter or sister. In short, India prefers men to have resources and women to be beautiful virginal

ingénues. As a result, films did not contain a great deal of sexual content as such; it is difficult to have sex scenes in a film when one half of the couple must remain chaste and virginal. In addition, no actress hoping to have a major film career would dare be filmed in a sex scene. So how does Indian film convey "sexiness"? Instead of actual sex, films have multiple dance numbers where the actress could dance or dress more sexually. Bollywood clichés include a sari that gets drenched in the rain and clings to her body, the man grabs her skirt and it rips or takes her scarf off, or she is dancing without knowing he is there. All these devices protect her innocence; she is *unintentionally* sexy. Films also use an item song (Kumar, 2017); a musical number that spotlights an ingénue. She is the "item girl" ("item" is a term for a sexy woman) so female sexuality is still depicted. Item songs have little to nothing to do with the plot, and neither do item girls; they appear, dance sexily, and then disappear.

Major dramatic tropes in Indian cinema include women having to choose between rich and poor suitors (and the importance of male suitors having resources) men competing for young, beautiful, virginal women, and lecherous male villains attempting to take advantage of innocent ingénues. Indian cinema heavily relies on the evolutionary concepts of intrasexual (particularly male) competition and the male desire for virtuous women. One of the major themes in Hindi and other films is the vital importance of the ingénue's innocence, chastity, and virginity. Khan and Taylor (2018) found female characters were trusting, empathetic, emotional, soft spoken, and the object of male desire. The lesson often "taught" is that a girl must be very cautious, protected, and selective; one wrong decision and her purity, and her future, would be destroyed. Khan and Taylor (2018) also found women to be helpless, suffering, intimidated, and lonely. These themes did not change over the ten-year span of their sample. They also found that violation of these norms leads female characters into trouble. Men do not have this issue.

For an example of what type of film is successful in a country of a billion people, the film that immediately comes to mind is *Dilwale Dulhania La Jayenge* (loosely translated "the brave hearted wins the bride"). Released in 1995 and starring Shah Rukh Khan and Kajol, it became the biggest release of the year and the second biggest release of the decade, and it has continued on to become one of the highest-grossing Hindi films ever. It has been called Bollywood's definitive romance, and one theater showed the film continuously for twenty-five years (Seta, 2020). The plot, put most simplistically: naughty boy (Raj) and virtuous girl (Simran) meet while abroad, boy is assertive and falls in love with girl quickly, girl is modest and steadfast, she eventually falls in love as well, but the girl's father does not think the boy is acceptable, takes the girl back

to India, and promises her to another. One of the key points throughout the film is the girl's modesty; she does not sleep with the boy and maintains her "honor." Her honor is the key point of drama in the film. One reviewer stated possible reasons for the film's success, including "Perhaps it's the way in which the film *artfully reaffirms the patriarchal status quo and works for all constituencies*" (italics ours). Khan and Taylor (2018) found that adherence to gender norms led to better life outcomes for female characters, so it will not surprise anyone that Simran's modesty and honor leads to a "happy ever after" for she and Raj.

Given this focus on male preferences and mating strategies, it is important to discuss female-oriented and -dominated media, namely, romance novels and subsequent films. As we have already reviewed, female preferences involve greater long-term commitment (Buss et al., 1990) from men with more resources (Buss et al., 2001; Kenrick et al., 1990) and status (Li, 2007), as well as possessing genetic quality (Thornhill & Gangestad, 2008). Fisher and Cox (2010) found that depictions of lead male characters in romance novels match these preferences; they are tall, masculine, strong, well built, rugged yet refined, confident, clever, and rich. The heroine is usually not described as beautiful by the author but certainly described as such by the hero. What she is always to the hero is irresistible (Gorry, 1999). You will notice these are the same themes found in the analysis of Hindi films.

As Thornhill and colleagues point out, these qualities may come from more than one man. So it is not surprising that the plots of most female-centered romance novels and films focus on long-term mating with some short-term entanglements. Cox and Fisher (2009) needed to look no further than the novel covers to find this emphasis; titles included lucrative and prestigious occupations such as doctors, royalty, and CEOs, and occupations that would need significant physical abilities, such as cowboys, law enforcement, or soldiers. Love triangles, where the woman must choose between commitment or high-quality genes, are a common trope (see previous mention of Jean Grey's dilemma). These romances almost always end with a long-term commitment, even from the "lone wolf" or womanizing male character (Fisher & Cox, 2010). This plot twist is a key one, as the woman is able to acquire a man who has both the high genetic quality of a "cad" and the steadfast commitment of a "dad." As Fisher and Cox (2010) state, "a Harlequin plot can be summarized as follows: boy meets girl, boy has to do something to live up to girl's expectations, girl falls for boy, and they live happily ever" (p. 308). Not surprisingly, this is also seen in *Dilwale Dulhania La Jayenge* except given the practice of parental matchmaking in India, the boy must also do something to live up to girl's *family's* expectations, then the happy ever after can commence.

The Wild and Woolly World of Pornotopia

If aliens came to earth, what would they learn about human sexual psychology from pornography? Commercial pornography is a multibillion-dollar global industry whose characteristic features have been shaped in free markets by the choices made by hundreds of millions of consumers who have voted with their money. While commercial DVDs and films have decreased in number over the last ten to twenty years, internet pornography sites are a booming business. Pornography consumption occurs in every industrialized society, which can be seen in the data reported by internet pornography giant Pornhub (2019) in their year-end review. In 2019, there were more than forty-two billion visits to PornHub worldwide and thirty-nine billion searches performed.

Pornography is an artifact of male sexual desire. The most commercially successful, or most frequently consumed, material taps into basic aspects of male mating psychology, in particular, that part of male mating psychology that is directed toward short-term mating. The world of pornography is one in which sex is pure gratification, with no courtship costs, commitment, lasting relationships, or mating effort. The women are eager to have sex with strangers, easily aroused, always orgasmic. The focus is not on plot but on the sex acts themselves, emphasizing the faces and bodies of the female participants (or male participants in the case of gay porn). It is testament to the visual nature of male sexuality. The females featured in pornography display cues of high mate value in that they are generally young and attractive, ideal short-term mating partners (some exceptions to the ubiquitous youth will be discussed later).

Given that men are the primary consumers of online pornography, it is expected that their mating psychology is clearly evident in the content. Why is it that men (for the most part) look for young but not elderly women when searching online pornography? It is because youth is a characteristic that indicates fertility and high reproductive potential, which men prefer without being conscious of the underlying rationale. For example, Ogas and Gaddam (2011) reported that the most frequent search term (looking at the results of a general search engine) was “youth” followed by gay, MILFs, breasts, and cheating wives. No one is likely to be surprised that men spend time looking at breasts (Widman et al., 2019). Pornhub’s global most searched terms of 2019 included “teen” indicating youth, as well as such female body parts as “big tits” and “big ass,” features often associated with fertility (Pornhub, 2019).

The popularity of MILFs might be a bit more surprising. However, Millford’s (2013) study of adult film star statistics indicates that the average age of female stars in MILF films is thirty-three, all exhibiting fertile/youthful-looking body

shapes, lustrous hair, and so on. In addition, some researchers have documented that women in their thirties have more sexual fantasies, are more likely to engage in casual sex, and exhibit a greater willingness to have one-night stands (Easton et al., 2010). These are all characteristics that would be highly desirable in a short-term mate, and younger men often exhibit an interest in women with sexual experience who will improve their own sexual skills, particularly when they are not looking for a long-term sexual partner (Kenrick et al., 1996). The top Pornhub.com searches of 2019 included "MILFs" and "Stepmom." When Pornhub separates porn-category-viewing popularity by gender, "Mature" and "MILF" are #8 and #10 for women and #3 and #4 for men. With regard to Ogas and Gaddam's (2011) finding about the popularity of cheating wives, it was not reflected in the 2019 Pornhub top twenty statistics, though it did appear in the 2017 ones. One study that examined infidelity intentions as well as actual infidelity behavior and their relationship to specific pornography preferences indicated that for men and women, intentions and actual infidelity were both associated with preferences for group sex scenarios in porn (Salmon et al., 2019). In 2019, gangbang was #12 in women's favorite categories while threesome was #10 for men. However, both categories were viewed more frequently by women than men (Pornhub, 2019).

Using the Pornhub Year in Review data for 2017, Salmon et al. (2020) examined the most sought after porn actors and actresses. PornHub released the names of the most searched actresses in 2017, both globally (top twenty searches) and across twenty separate countries (top five searches for each country). These twenty countries (Argentina, Australia, Belgium, Brazil, Canada, France, Germany, India, Italy, Japan, Mexico, Netherlands, Philippines, Poland, Russia, South Africa, Spain, Sweden, United Kingdom, and United States) account for 80 percent of the daily traffic on the Pornhub website (https://www.pornhub.com/insights/2017-year-in-review). In total, there were 108 top searched names for fifty actresses. This overlap shows that although there is some cultural variability, a number of women are searched repeatedly regardless of country, indicating cross-cultural similarity in preferences. The body measurements of these women can also be obtained through biographical websites and this can give us more information about male porn preferences. Over the 108 most popular searches, the average bra cup size was a D, the average waist size was approximately twenty-five inches, and the average hip measurement was greater than thirty-six inches. When the top twenty searched women in the world were examined, waist-to-hip ratio was .687 and when the top five women who appeared the most in rankings across the twenty listed countries were measured, their waist-to-hip ratio was .669. This figure is

definitely in the super stimulus range based on work by Platek and Singh (2010) on clear indicators of youth and fertility.

Gay male pornography accounts for approximately one third to one half of the $2.5 billion commercial adult industry (Thomas, 2000) and Pornhub has a separate site tailored to a homosexual male audience, PornhubGay. Salmon and Symons (2001) suggested that there were no significant differences between gay male pornography and pornography produced for heterosexual men (other than the sex of the actors) because they both tap into basic male sexual psychology, which does not differ on the basis of sexual orientation (Bailey et al., 1994). Salmon and Diamond (2012) explored this by comparing homosexual and heterosexual porn aimed at a male audience in terms of the activities portrayed and indeed found very few differences between them. Interestingly, the most viewed category on PornHubGay is "straight guys" followed by "daddy," "bareback," "black," and "big dick." A number of researchers have suggested that gay men's preferences, much like those of heterosexual men and women, can be influenced by mating context such that attractiveness matters more when short-term mating is being pursued (Valentova et al., 2017; Varangis et al., 2012) and muscular masculine men (perhaps partly being captured by terms like "straight guys," "daddy," and "big dick") are particularly desirable. Gay men in general have also been reported to have greater interest in casual short-term sex, which is the typical focus of porn whether targeted to a homo or heterosexual male audience (Bailey et al., 1994; Lippa, 2007; Gobrogge et al., 2007); —no-commitment, low-cost sex with a variety of physically attractive partners.

Exceptions That Prove the Rule … Slash Fiction and Yaoi

Before considering how slash and yaoi are exceptions that prove the rule, we should first explain what they are. Slash is a genre of male–male romantic/sexual stories based on fictional characters in which both members of the romantic pairing are expropriated male media characters (Salmon & Symons, 2001). Popular pairings have ranged from Kirk and Spock from *Star Trek*, to Sherlock Holmes and John Watson, or Steve Rogers and Bucky Barnes from the Marvel universe. Yaoi is a similar genre that started in Japan where the focus is also on homoerotic and romantic relationships, in this case between two young men or boys. Yaoi is primarily marketed to a female audience and the majority of writers are also women, much as is the case for slash fiction (Magera, 2019; Thorn, 1997). Both of these genres are smaller than female-oriented romance more generally or pornography, but because of their smaller, somewhat more esoteric nature, they are prime candidates for hypothesis testing because their similarities

with other genres, such as romance, highlight essential features of female mating psychology while their differences may suggest hypotheses about individual or cultural differences. First we will discuss slash as a subgenre of romance, followed by a consideration of whether yaoi is also a subgenre of romance and evidence they provide about female sexual psychology.

Slash is very similar to mainstream romance novels. For example, a stash story is, in essence, a love story in which two males, often long-term friends and/or partners, come to the realization that they are in love with each other. Slash stories typically have a happily-ever-after ending, the establishment of a permanent romantic and sexual bond. When they don't, authors typically warn their readers. While slash ranges in explicitness from PG to explicit, the majority of the sex occurs within this committed relationship and the emotional meaning is typically emphasized, much as it is in explicit romances or erotica. In addition, many stories focus on the first time a pair "consummates" their relationship as well as the things that lead up to their "discovery" of their love for each other, which is also the majority of the plot of most mainstream romance novels. They are tales of finding a high-quality mate and entering into a committed sexual and romantic relationship, the goal of long-term mating strategies (Buss, 2016; Cox & Fisher, 2009; Salmon & Symons, 2001).

The majority of slash pairings also contain one if not two physically attractive men much as the heroes of romances are typically portrayed as physically fit, often dominant men whose softer side is directed toward the heroine. Slash protagonists are also typically powerful men, whether that power is demonstrated via physical display or other prowess. For example, the top five pairings on AO3 for 2019 (Archive of our Own which is an online archive for fan fiction, including slash, femslash, heterosexual relationships, and nonsexual stories) are all male–male pairings. They include, in order of number of stories archived, Castiel/Dean from *Supernatural*, Holmes and Watson from the BBC's *Sherlock*, Derek/Stiles from *Teen Wolf*, Steve/Bucky from the Marvel universe, and Draco/Harry from the *Harry Potter* books and films. Many researchers have noted that the heroes of romance, and of slash, embody traits attractive to females from an adaptive perspective, including genetic quality, ability to acquire resources, dominance, ability to protect, and a strong love/commitment to the heroine (Bech-Sørensen & Pollet, 2016; Buss, 1989; Fisher & Cox, 2010; Gorry, 1999; Radway, 1984; Salmon & Symons, 2001).

Evolutionary approaches to mate preferences have often used survey data and information on the relative ages of married couples to examine male preferences for younger wives and female preferences for older husbands (Bech-Sørensen& Pollet, 2016; Kenrick & Keefe, 1992; Kenrick et al., 1996). Conroy-Beam and

Buss's (2019) review of the literature on age and mate preferences highlights that, for females, age is relevant to long-term mate attractiveness because of its relationship to resources and cues to resource acquisition as well as sperm quality. Resource acquisition for relatively young males increases with age making slightly older males attractive to young women. At the same time, female fertility is also influenced by age as fertility declines with increasing age, the peak being in the mid-twenties. Interestingly, while the majority of slash pairings feature men who are relatively similar in age, one of the top three pairings (according to AO3) in Harry Potter slash fandom is Harry and Professor Snape. The top three are Harry/Draco (as mentioned previously, it is in the top five overall), Sirius/Remus, followed by Harry/Snape, sometimes referred to as Snarry. This is a pairing with an older powerful authority figure male and a younger one, who later achieves significant power of his own. Although many consider the student–teacher sexual relationship to be deviant and socially unacceptable, and some Snarry authors set their stories after Harry turns eighteen, crushes on teachers are quite common among teenage girls and boys and have been recurrent themes in television, novels, films, and music. Many Snarry writers and readers report finding the teacher–student dynamic appealing (Duggan, 2017), and it is not an uncommon theme in other forms of fiction (Pierson, 1986). In the real world, these relationships are highly problematic but in fantasy fiction they most likely reflect young females' interest in older more powerful, experienced men with resources and status. The sexual appeal of an older female teacher to a teenage male is also a common theme in popular culture as expressed in the English band Busted's song *What I go to School for* with the following lyrics: "I love a member of the staff/And I fight my way to the front of class/To get the best view of her ass." Music loving Snarry fans matched scenes of Snape and Harry to go along with the lyrics in a video available on YouTube.

In many ways, yaoi is similar to slash and romance. Known also as "boys love," it is one of many genres that are part of the artistic/literary form known as manga. They are found in both professional publications as well as self-published dojinshi which may include characters borrowed (as in slash) from other media including other manga, video games, and Western television and film. There is a long history of male same-sex romance in Japan (Magera,2019; Turner, 2018) and, unlike slash, yaoi is sold in mainstream bookstores and displays often feature, in addition to two young males, an older male (seme) with a younger smaller one (uke). The trope of the seme or more dominant insertive partner and the uke or receptive partner is well-known. There have been dojinshi featuring Obi-Wan/Qui-Gon (from *Star Wars*) in that trope, which was a popular

slash pairing at one time as well, though Obi-Wan is typically drawn younger than the actor was in the film.

In some ways, yaoi has even more traditional romance conventions than slash does, partially due to the seme/uke role division which is less common in slash (or at least it is less consistent in terms of which characters take on more aggressive vs receptive roles). However, the essential components and progress of the mainstream romance such as barriers, developing attraction, recognizing attraction, and consummation/commitment are found in the majority of popular yaoi (Pagliassotti, 2010). Interestingly, one difference between yaoi readers and many romance readers and slash fans is the importance placed on a happy ending. Radway's (1984) study of romance readers reported that the most important feature in romances was a happy ending with the second the slow development of the love between hero and heroine. But yaoi fans reverse this order with the happy ending in second place. Both groups, however, also add to their lists scenes of the couple after they are together, and the yaoi fans also prefer explicit sexual illustrations more than the romance readers (Pagliassotti, 2010). Many slash readers also seem to enjoy explicit descriptions of the sex in their fiction as seen in the popularity of those stories on AO3 labeled as "mature" or "explicit." However, the emotional intensity of those scenes whether they be fictional or artistic in depiction is undeniable.

So if slash and yaoi share so much with mainstream romance, why do women consume their stories and not just romance? What is the added appeal here? A number of researchers have suggested a number of possibilities including individual differences, as not all women consume slash or yaoi when aware of their existence. With regard to slash, Salmon (2015) and Salmon and Symons (2004) suggested that slash might be particularly appealing to tomboys or females with greater prenatal testosterone exposure. Salmon (2015) tested this using adult 2D:4D digit ratios as a proxy for prenatal testosterone exposure and reported that slash readers had lower 2D:4D ratios indicative of higher prenatal testosterone exposure. The action-adventure, shared danger aspect of many slash settings may have particular appeal to some women in addition to the appeal of the tested committed bond between the male lovers. Both slash and yaoi readers sometimes articulate that heterosexual romance novels can be unsatisfying and that slash and/or yaoi is better in some undefined way. Interestingly, the egalitarian nature of many slash pairings which are often cited as having significant appeal to slash readers is less apparent in many yaoi works because of the seme/uke distinction which is sometimes cited as a reason slash fans are not always yaoi fans (Pagliassotti, 2010; Zhao & Madill, 2018; Zsila et al., 2018), especially when the uke is particularly feminized which may reflect

differences in Japanese versus Western conceptions of masculinity. More analysis of popular works in both genres as well as popularity differences across cultures may add additional insight to individual differences, while still highlighting the essential aspects of female sexual psychology found in the majority of popular culture in terms of long-term mate preferences and relationship ideals. As Zhao and Madill (2018) note in their comparative study of Chinese and Anglophone yaoi fans, an everlasting romantic relationship is the essential ingredient.

Final Thoughts

In many ways, the study of human mating psychology and behavior is one that has attracted much interest but that, at times, is challenging to study because of social desirability bias in survey methods, ecological validity in laboratory settings, and other factors. Adding unobtrusive measures, including the portrayal of mating in popular culture, can provide additional supportive (or contradictory) evidence in addition to the many existing research methodologies. Universal features of popular culture can highlight human universals in mating psychology. One area still largely unexplored is how cross-cultural and individual differences in popular culture product preferences can inform us about the sources of variation in individual mating strategies and the environmental factors that influence them.

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CHAPTER
35

Evolutionary Mismatch and Human Mating: Understanding the Mating Mind in the Modern World

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Abstract

Evolutionary mismatch is the idea that adaptations are operating in an environment that differs from the environment in which they were shaped by natural selection. Research on human mating from an evolutionary perspective requires thoughtful consideration of the evolutionary mismatch of modern subjects of study and their mating adaptations. In this chapter, I describe the concept of evolutionary mismatch and how it relates to the environment of evolutionary adaptedness. I provide examples of the importance of considering evolutionary mismatch that relate to some of the most well-studied domains of human mating including attraction, long-term relationships, sexual conflict, and sexual dysfunction. I advocate for the study of diverse populations as a tool to develop knowledge on the range of ecological conditions in which humans live and have lived, which is key to understanding evolutionary mismatch. I conclude by emphasizing the necessity of accounting for evolutionary mismatch when trying to understand underlying universal psychological design, and ultimately human nature.

Key Words: evolutionary mismatch, human mating, attraction, arousal, long-term mating, sexual dysfunction, sample diversity

Vaccines, airplanes, megacities. Commercial agriculture and food supply chains. The internet, dating apps, and social media. Each of these features of our modern environment, and many others, contribute to stark differences in modern

ecologies compared to the range of environments in which people lived for most of human evolutionary history. The focus of this chapter is on evolutionary mismatch, which occurs when adaptations—psychological, physiological, behavioral—are operating in an environment that differs from the conditions that shaped their design. Evolutionary mismatch has been discussed since the early days of the modern evolutionary social sciences (Symons, 1979; Tooby & Cosmides, 1992). However, recent work on evolutionary mismatch has focused on more precisely elucidating evolutionary mismatch concepts, including defining dimensions of mismatch, identifying specific characteristics of modern people and ecologies that have important mismatch implications, and ascertaining which domains of human behavior would benefit from being viewed through the lens of evolutionary mismatch (Goetz et al., 2019; Gurven & Lieberman, 2020; Li et al., 2018; van Vugt et al., 2020).

This chapter contributes by specifically addressing evolutionary mismatch as it relates to research on human mating adaptations. First, I address the concept of the environment of evolutionary adaptedness (EEA) and its importance in conceptualizing evolutionary mismatch. Then, I review existing research within some well-studied domains of human mating. The reviewed studies exemplify the importance of thinking about evolutionary mismatch in relation to human mating adaptations and illustrate why thinking about evolutionary mismatch is central to developing our understanding of human nature. I argue that diversifying populations of study is a key methodological tool that researchers can employ to test and evaluate evolutionary mismatch hypotheses.

Mismatch and the EEA

Evolutionary scientists use the term “EEA” roughly to refer to the environment to which organisms have adapted. The concept of the EEA when applied to human evolution is often confused with a specific time and place, namely, the African savannah during the Pleistocene. The more precise, technical definition of the EEA demonstrates why this is incorrect. The EEA is the statistical composite of selection pressures that existed during an adaptation’s development that shaped the adaptation’s design (Tooby & Cosmides, 1992). Inherent to the concept of the EEA is that it is adaptation specific. Different adaptations were uniquely shaped by different selection pressures—the structures of the eye evolved in response to variations in the electromagnetic spectrum; olfactory systems were shaped by the fitness benefits of detecting different airborne chemicals. The time spans during which different adaptations were shaped also vary. Newer adaptations, such as those related to language-

acquisition and production, have a shorter EEA than adaptations that evolved in response to comparatively older adaptive problems, such as avoiding venomous snakes. Furthermore, existing adaptations are still subject to the process of evolution by natural selection. Should the selection pressures and their fitness consequences change, then it is possible, and expected, that the adaptations in future generations of a species would differ from the adaptations in their present form. Scientists addressing questions of evolutionary mismatch are often focused on understanding an organism in its current form, and how its adaptations operate in the current environment. Understanding the EEA for a particular adaptation, then, is necessary for hypothesizing about how that adaptation will work (Lewis et al., 2017).

Consideration of adaptations' EEAs is fundamental for assessing evolutionary mismatch for at least three interrelated reasons. First, understanding how an adaptation works in the present requires understanding the forces that shaped it. Selection pressures mold adaptations, determining (1) which cues, or input, an adaptation responds to; (2) how that input is processed and what decision rules regulate that adaptation's functioning; and (3) the adaptation's final physiological, neurological, cognitive, and behavioral output (Tooby & Cosmides, 1992). Selection pressures shape the flexibility of adaptations and their possible ontogenetic trajectories (Barrett, 2014). Addressing questions of evolutionary mismatch starts with the process of deconstructing the underlying design of an adaptation (Goetz et al., 2019; van Vugt et al., 2020). Only then can a researcher hypothesize about how an adaptation will operate in the present.

Second, knowledge of an adaptation's EEA provides insight into why an organism's current behavior may appear curiously "maladaptive," or why observed behavior may have no apparent modern fitness benefit—a key focus of much of the literature on evolutionary mismatch (Gurven & Lieberman, 2020; Li et al., 2018). Consider a woman who uses hormonal contraceptives and intends to remain childless but still scrutinizes a man's financial prospects when assessing him as a mate. Because women historically incurred the greater fitness costs associated with pregnancy, breastfeeding, and subsequent childcare, their mate preference adaptations are calibrated to evaluate and value indicators that a partner will be able to contribute resources to her and her offspring to help offset her obligatory investment (Buss, 1989; Trivers, 1972). However, this particular woman will never benefit in fitness currency by preferentially selecting mates with greater wealth or resources because she will never reproduce. Additionally, her choosiness could impede her ability to attract a mate at all, to the detriment of her long-term happiness (Apostolou et al., 2019). In this example, knowledge of the selection pressures that shaped mate preferences adaptations help explain

modern women's decision-making strategies even when the outcomes of those decisions have no apparent fitness benefit and negatively affect their life satisfaction. Even a woman's decision to use hormonal contraceptives and remain childless may be better understood by thinking about her adaptations' EEAs. Any adaptations that function to motivate women to control and plan reproduction, invest in their own status and resources, or favor decisions that protect their health and well-being evolved in an environment in which modern contraception was not an option. Choosing to remain childfree significantly limits the pathways through which a person's genes can propagate themselves into future generations (to reproduction via their genetic relatives), but the design of adaptations motivating such a choice are understandable if we consider their EEA.

The example of modern contraceptive technologies highlights a third reason why assessing the EEA is necessary. Knowledge of ancestral selection pressures provides insight into which features of an organism's current environment are truly novel and may help researchers better understand how and why adaptations respond to, or are influenced by, novel environmental cues. Research on racial categorization provides an illuminating example. Evolutionary psychologists have argued that ancestral humans rarely would have encountered other humans whose skin color would have differed substantially from their own (Kurzban et al., 2001). That many modern people live in racially heterogeneous ecologies is a mismatch from their adaptations' EEAs. However, people easily engage in race-based categorization—so why and how are our adaptations responding to this novel environmental feature? One hypothesis is that humans evolved an alliance detection system, a suite of adaptations that function to categorize and track cooperative alliances (Kurzban et al., 2001; Pietraszewski et al., 2014). Contemporary people learn that race is one indicator of social alliances, triggering the alliance detection system to attend to the cue of variation in skin color, even though this specific cue was not one that shaped the evolution of alliance detection adaptations. Framing the question of racial categorization as one of evolutionary mismatch generated hypotheses about which adaptations may be responding to race in our modern environment and revealed the circumstances under which racial categorization is more or less likely to occur (Kurzban et al., 2001; Pietraszewski et al., 2014).

Evolutionary social scientists rely on a multitude of sources of evidence and methods to hypothesize about features of human's ancestral past, including cross-species comparisons, archaeological records, studies of the genetics of humans and nonhuman animals, and data from small-scale and hunter–gatherer societies. However, our knowledge of the EEA of adaptations involves some

degree of uncertainty because we are hypothesizing about past selection pressures that we cannot directly observe. This uncertainty has implications for evaluating evolutionary mismatch. Scientists may be able to make stronger claims about the differences between an organism's current environment and their adaptation's EEAs for some adaptations rather than others. For example, Volk and Atkinson (2013) marshalled substantive evidence to support the claim that modern living, especially modern medicine, has drastically reduced infant and child mortality rates in modernized cultures. Mismatch discussions related to differences in infant and child mortality are more solidly grounded than those that rest on more speculative claims about differences between now and the past that are derived from evolutionary-inspired hunches rather than built on multiple sources of data and evidence. Therefore, claims of mismatch rest not only on what researchers think they know about the EEA of adaptations but also on how *certain* they are about the existence and impact of past selection pressures.

Mismatch in Mating

In this section, I will address examples of specific hypotheses, theories, and scholarship related to evolutionary mismatch and mating. I have organized these examples by subfields within human mating research. Rather than providing a thorough review of all the literature and important research within each domain, I have curated examples that demonstrate the importance of EEA-based analysis of adaptations and evolutionary mismatch and provide insights that can be applied more broadly.

Attraction

Mate attraction is one of the most commonly studied topics in the evolutionary social sciences. Barrett (2020a) analyzed the keywords associated with articles published in *Evolution and Human Behavior* from 2015 to 2020 and found that "attraction" and "attractiveness" were some of the most frequently used. The effort invested in studying mate attraction is warranted. Attraction, desire, and other motivating emotions are the impetus for mating behavior in sexually reproducing species and evolutionary success and fitness are contingent on reproductive success. However, psychological mechanisms related to mate attraction evolved in an environment mismatched in numerous ways from the environment of people studied now. That many subjects of study, for example, live in areas of high population density, are geographically separated from close kin, and have high degrees of autonomy may profoundly influence the processes

by which they select mates. One mismatched feature present in the environment of the majority of modern people of study that has specific implications for understanding attraction is ubiquitous exposure to imagery of sexually appealing people through mass media, social media, and pornography.

Decades of research have demonstrated contrast effects in our judgments of others' attractiveness—for example, a moderately attractive target is perceived as less attractive if the rater is first exposed to a highly attractive target compared to if the rater is first exposed to a moderately attractive or unattractive target (e.g., Burleson et al., 2016; Kenrick & Gutierres, 1980). These studies provide evidence that judgments of physical attractiveness are not derived from comparisons to a fixed standard but are relative assessments anchored to internal reference points that can be updated based on context and exposure to novel stimuli (Mussweiler, 2003).

One concerning possibility is that people who are bombarded with imagery of sexually appealing others develop a skewed sense of the attractiveness of their peers, and of themselves. Psychological mechanisms that assess attractiveness evolved in an environment where there was no need to distinguish between inaccessible, photoshopped models and attainable potential mates in your geographic area. With the rise of social media, these lines have become even more nebulous. Casually scrolling through Instagram barrages mating mechanisms with handpicked images of celebrities, often engaging in mundane "relatable" activities, alongside images of people the user actually knows. And even the imagery of the user's real acquaintances has been carefully selected and manipulated to showcase the person at their best. Heightened exposure to highly attractive people via mass and social media may trick our mating mechanisms into perceiving that we live in a world saturated with highly attractive people. A person's actual options for mates may pale in comparison to this landscape of people perceived as highly attractive, happy, and successful.

A direct consequence of developing biased attractiveness standards is that more realistically attainable mates may seem less attractive, and subsequently be less pursued. In support, Bhargava and Fisman (2014) analyzed 7,684 yes-or-no decisions made by more than four hundred participants across sixteen speed-dating events. They found that men in particular were less likely to say "yes" to a potential partner after first conversing with a more physically attractive woman. People are aware that their standards contribute to their inability to find a desirable partner, and that others' similarly high standards impact their own chances of someone wanting them. Apostolou et al. (2020) found that single Americans reported both being "too picky" and "not a desirable mate" as top reasons for their singleness. In Western countries, people are marrying later in

life, and less (e.g., Kreider & Ellis, 2011). One contributing factor to the delay and decrease in long-term partnering may be the disconnect between a person's viable options and their distorted perception of the attractiveness of the pool of potential mates.

Human mating psychology evolved in a competitive landscape and mate attraction inherently requires competing against same-sex others. Yong et al. (2016) explicitly used evolutionary mismatch thinking to hypothesize about how extreme exposure to attractive others affects intrasexual competition, specifically in women. They argued that because men place a greater premium on physical attractiveness in mate attraction and selection, the virtual deluge of attractive same-sex others may acutely trigger intrasexual competition in women. They outline a number of outputs of competition mechanisms that may have been functional ancestrally but lead to dire consequences in our mismatched environment. For example, low mood and feelings of inability, powerlessness, and hopelessness in response to a defeat may have usefully prevented an individual from continuing to engage with a competitor, risking injury, death, or greater reputational damage. Retreating affords the defeated individual time to recuperate and reassess their capabilities before another contest. As a consequence, modern women exposed to a stream of attractive women against whom they perceive they are constantly "losing" may experience clinical depression. Yong et al. (2016) also provide rationale for how virtual intrasexual competition may trigger other ancestrally functional mechanisms that now contribute to self-esteem deficits and disordered eating. Although their analysis focused on women, they argued that the same logic applies to men with respect to virtual exposure to competitors displaying characteristics that women privilege in mate selection, such as financial prospects and status.

People who developed, and are currently operating, in an environment with pervasive exposure to attractive people are an evolutionarily anomaly, which has implications for the conclusions researchers can draw when using them as a source of data. At a minimum, the mismatch of research subjects suggests researchers must exercise caution in implying that any observed behavior, or mechanism output, is functional or fitness enhancing in the modern environment (Tooby & Cosmides, 1992). Additionally, features of modern environments may produce mating-related decisions or behavior that are uniquely a product of mismatch. For example, attraction and mate selection may be influenced to an unprecedented degree by the process of making constant comparisons between known and new mate options and competitors. This could mean the psychological mechanisms responsible for such comparisons play more of a role in producing mating decisions now than they would have in ancestral

environments, where mating pools were more stable and limited. Another possibility is mechanisms that function to sort and compare many options evolved for decision-making in another domain but have been co-opted for mating in our modern environment (Goetz et al., 2019). Such suggestions are certainly speculative, but they highlight the necessity of taking evolutionary mismatch seriously when attempting to draw conclusions about the evolved design of the mind.

Exposure to mass and social media is not the only way in which many of the people we study are mismatched that has implications for attraction and attractiveness. For example, many modern people live in densely populated areas, affording them far more options for mates than would have existed ancestrally. Western young adults, especially women, have far more autonomy in their mate choice than their ancestral counterparts had (Goetz et al., 2019). Each of these mismatched characteristics may differentially affect the operation of mating mechanisms and differentially shape the conclusions researchers can derive regarding psychological mechanisms related to attractiveness and attraction. Identifying mismatched characteristics and hypothesizing which may have significant impacts on the development and operation of mating mechanisms are essential to conducting research on attraction, and human mating in general.

Long-Term Relationships

Marriage is cross-culturally universal and researchers have hypothesized that humans have evolved suites of adaptations the functioned to form and maintain long-term relationships (Conroy-Beam et al., 2015; Jankowiak & Fischer, 1992). Recently, researchers have posed novel hypotheses about how mismatched features of many modern environments interact with long-term mating mechanisms in ways that may substantially impact romantic relationship quality and desire to long-term mate. Mismatched features identified by researchers include smartphones, greater autonomy in mate choice, and unprecedented materialism.

Sbarra et al. (2019) proposed that smartphones perturb two key processes that lay the foundation for close relationships: self-disclosure and responsiveness. They argued that smartphones hijack relationship formation mechanisms that motivate self-disclosure, which functions to bolster trust and intimacy between partners. Because social media platforms provide ample opportunity for self-disclosure, people can be captivated by their smartphone, devoting time and attention to virtual relationships at the expense of face-to-face interactions and

connections. Furthermore, social media apps are tailored to elicit low-cost responses in the forms of "likes," comments, replies, and shares. People caught up in a cycle of self-disclosure and low-quality responsiveness on social media can devote significant time and effort to these pursuits without the payoff of developing real close relationships. Evolutionary mismatch can explain both why people are motivated to interact with smartphones in this way and why this leads to dissatisfaction and poor relationship outcomes. Although Sbarra et al. (2019) acknowledge that self-disclosure and responsiveness elicited via smartphones could facilitate relationship formation and maintenance with partners in person, they argue that extant research indicates that smartphone usage has a net negative effect on social connectedness and well-being.

Lack of kin and parental influence in mate choice is another characteristic of many modern societies that has been hypothesized to contribute to difficulties in establishing and maintaining long-term relationships (Apostolou, 2015). Parents prioritize different traits in their offspring's mate, preferring potential partners who can provide social and economic capital, while children place a greater concern on a potential mate's attractiveness and qualities hypothesized to be associated with genetic quality (van den Berg et al., 2013). If ancestral mate choice occurred under the conditions of parental influence—via methods ranging from direct selection of an offspring's mate to parental manipulation of offspring mate choice—modern people selecting mates autonomously may be less likely to choose a partner with whom they will be able to develop a stable, lasting bond (Apostolou, 2015). However, it is also possible that greater autonomy has the opposite impact, and promotes greater compatibility among partners because offspring are able to make mating decisions that reflect their sole preferences and not those of their parents (Goetz, et al., 2019).

While the previously summarized research addressed evolutionary mismatch and close relationship maintenance and development, other research has examined how evolutionary mismatch concepts may be essential to explain recent reductions in *interest* in marriage and having children. Li et al. (2015) examined the relationship between materialism and attitudes regarding marriage and family. They found that the more people derived happiness and status from material goods, the more negative their attitudes were toward marriage and having children. In one of their studies, one subset of participants read a passage that described shopping for luxury and high-end goods. They found that this "materialism priming" increased materialistic attitudes, and was then related to the expected reductions in interest in marriage and children. Li et al. (2015) argued that modern-day materialism may be caused by mechanisms that evolved to motivate humans to acquire status and signal status to others. However, in an

environment in which resources can be endlessly acquired and stored as money, and technological advances allow for an ever-changing medley of new status symbols, these status mechanisms usurp other motivations. Cash economies also generate greater variability in resource holdings. Those who already have more money than they and their progeny could ever spend continue to amass wealth and display markers of their extreme prosperity. Those with less experience inequality of far greater magnitude than ever could have been experienced ancestrally. In such an environment, people are consumed by the need to acquire the new best thing and devalue pursuits that would detract from their ability to do so, such as marrying and having children.

The summarized research provides examples of the overt application of evolutionary mismatch thinking to develop and test hypotheses about long-term mating psychology. One challenge is determining exactly which characteristics of a mismatch-laden environment actually have some causal effect on how mating mechanisms work or on mating outcomes. This is evident in the examples provided here. For example, Li et al. (2015) noted that their findings are consistent with another explanation drawn from life history theory, which has been applied within humans to explain individual differences in reproductively relevant trade-offs. Organisms fall on a slow–fast continuum in which a slower life history strategy is characterized by greater investment in somatic development and the production of fewer offspring who receive greater investment, and a faster life history strategy that involves faster, more frequent reproduction with lower parental investment (e.g., Del Giudice et al., 2016). Environments with stable resources and high social competition are associated with slower life history strategies, so the association between materialism and interest in marriage and children may be reflective of life history strategy in conjunction with evolutionary mismatch.[1] Additionally, variability in competition and materialism may co-occur with differences in other sources of mismatch, such as smartphone usage, greater autonomy in mate choice, and many other still-to-be-identified mismatched features of modern environments (Goetz et al., 2019). As research grounded in evolutionary mismatch thinking develops, one challenge will be sifting through all the possible elements of mismatch to pinpoint which are directly affecting how human mating mechanisms work. But the examples provided here are instructive in demonstrating how mismatch thinking is being currently applied within research on long-term mating to explain already known phenomena and to generate novel hypotheses about mating-related cognition and behavior.

Sexual Conflict

Sexual conflict and associated phenomena, including sexual harassment, intimate partner violence, and sexual assault are important topics, in no small part due to the devastating impact such events can have on individuals. Some degree of mating-related conflict is inevitable because people's individual sexual strategies and motivations do not always align. Sexual conflict emerges when the fitness consequences of a particular outcome differ between males and females. Adaptations and strategies in males and females, selected to benefit their own fitness, can generate traits and behaviors that are designed to influence the other sex, producing sexually antagonistic coevolutionary arms races. As a result, men's and women's sex-differentiated mating adaptations can generate strategies that interfere with one another (Buss, 2016). An evolutionary mismatch framework is useful for understanding modern contexts and predictors of sexual conflict. Furthermore, evolutionary mismatch thinking may prove indispensable in developing approaches to curbing undesired outcomes of sexual conflict, including harassment, intimate partner violence, and rape (Buss, 2021).

Workplace sexual harassment provides an example of sexual conflict that may be better understood by considering evolutionary mismatch. Modern employment settings are rife with evolutionary novelty. Numerous reproductive-aged men and women are compelled to spend many hours together, working collaboratively. Professional codes of conduct dictate that people behave collegially, interacting and conversing with opposite-sex others with whom they may not otherwise be interested in socializing. Women at work are separated from protective spouses and kin and, depending on the place of employment, may be in a minority. However, men's and women's mating psychology, which evolved under very different circumstances, is still operating in this novel environment. Men's short-term mating psychology, attuned to the presence of novelty and sexual variety, may be activated in workplaces in which there are dozens or hundreds of employees (Buss & Schmitt, 1993). Collegial interactions in which women listen attentively and smile politely can be misinterpreted as flirtation by men whose evolved bias to overperceive sexual interest is operating in the novel workplace setting (Haselton & Buss, 2000). And without protective "bodyguards" such as spouses or male kin, women may be perceived as easier targets who more likely to consent to, or be compelled to engage in, a sexual relationship (Buss, 2016). Of course, not all workplace sexual harassment can be attributed to men's psychological mechanisms misfiring in evolutionarily novel circumstances. But if some proportion of sexual harassment claims are rooted in evolutionary mismatch, then identifying mismatched features of workplaces, and educating employees about such mismatches, may meaningfully contribute to reducing mating-related workplace conflict.

The lens of evolutionary mismatch may also be informative in understanding more severe forms of sexual conflict, such as sexual assault. One obvious source of evolutionary mismatch is the existence and use of alcohol and drugs. Humans and other primates have historically consumed fermenting fruit and other plants with mind-altering effects; however, modern, human-produced, psychoactive substances can be consumed in far greater quantities and have more acute effects on inhibition, judgment, and decision-making (Dudley, 2002). A substantial number of sexual assaults occur when the victim, perpetrator, or both are under the influence (e.g., Abbey et al., 1996). In men, alcohol and drugs may increase the odds of perpetration through multiple routes, including affecting their perception of women's sexual interest and their propensity for aggressive behavior (Abbey et al., 1998). Women who have consumed alcohol or drugs are less able to physically defend themselves and communicate their lack of consent, and they display cognitive impairments that put them in greater danger of victimization, such as decreased risk detection (Loiselle & Fuqua, 2007). Men also perceive women under the influence as more vulnerable, which may make them more likely to be targeted by men implementing sexually exploitative strategies (Goetz et al., 2012). Even women's fears about sexual assault may reflect evolutionary mismatch and lead to them being less equipped to protect themselves. Although women are at greater risk of being raped by someone they know, they are more fearful of stranger rape, and engage in more precautionary behavior related to fear of stranger rape than acquaintance rape (e.g., Hickman & Muehlenhard, 1997; Warr, 1985). Low likelihood of stranger rape may demonstrate that women's evolved fear is functioning well in our modern environment, protecting women from the threat of modern-day stranger rape. However, if women's rape-related fears were shaped in an environment in which risk of rape by strangers from outgroups was a bigger threat, then their fears about rape are uniquely calibrated to protect them from stranger rape but less well-designed to protect them from acquaintance rape (Buss, 2016; Buss, 2021). Experiencing lower fear in response to the idea of acquaintance rape may leave women ill-prepared to protect themselves from the modern threat of acquaintance rape, contributing to its greater likelihood.

Sexual conflict is not evolutionarily novel, and not all instances of it should be characterized as evolutionary mismatch. But novel features of the environment may produce sets of circumstances that spark sexual conflict and may change the fitness outcomes associated with sexual conflict. Evolutionary mismatch thinking will help us better understand contexts and risk factors related to victimization and perpetration in instances of sexual conflict, and they can help us better understand the psychology leading to conflict in more

ambiguous situations where labels of victim and perpetrator are not so clear-cut. And this knowledge may be advantageous if it can be applied to develop interventions or strategies for reducing sexual conflict. Consider intimate partner violence, which has been well-studied on a global scale. Factors associated with decreased levels of lifetime intimate partner violence among women include less exposure to violence in childhood, secondary education in women, and social norms and laws that punish violence against women (Devries et al., 2013). Determining which evolutionarily novel features of societies are associated with lower sexual conflict provides insight into the types of policies that may be more effective in reducing societal ills like sexual harassment, intimate partner violence, and sexual assault.

Sexual Arousal and Dysfunction

Evolutionary mismatch thinking provides a framework for understanding how sexual arousal functions in men and women, and is crucial for understanding sexual dysfunction. A key insight that is only apparent through the lens of evolutionary mismatch is that dysfunction in sexual arousal, as defined by medical practitioners, clinical psychologists, pharmaceutical companies, mass media, and people experiencing sexual dissatisfaction, may not be indicative of arousal-related mechanisms malfunctioning. Physiological or psychological arousal mechanisms may be operating exactly as natural selection designed them to operate. However, elements of our mismatched, modern environment may shape our definitions of sexual dysfunction to reflect comparisons to modern standards and the subjective experience of distress, rather than that mechanisms are not working according to their species-typical design.

Men and women report different problems with their sex lives. In a nationally representative survey of US adults, early ejaculation and erectile difficulties were the most commonly reported problems among men (Laumann et al., 2009). Men's reported sexual dysfunction centers on their physiological ability to initiate and maintain sexual intercourse. Evolutionary logic explains why successfully executing sexual intercourse should be of particular concern to men. Male intromission and ejaculation are necessary for fertilization to occur, while analogous physiological processes in women are not. However, instances of premature ejaculation may reflect typical, and possibly adaptive, functioning, despite the discomfort or distress they cause.

Fast ejaculation has been hypothesized to be a feature of primate sexual intercourse, not a flaw (Hong, 1984). The average time between intromission and ejaculation in a number of primate species, including the closely related

chimpanzee, is under a minute. Hong (1984) argued that faster ejaculation may have served multiple functions among social primates and early hominids, including reducing the probability of being physically attacked by other males attempting to gain sexual access to a desired female and providing a reproductive pathway for subordinate males, who may only be able to successfully mate if the encounter is accomplished quickly. Therefore, it is possible that rapid ejaculation was inherited from a hominid ancestor and was maintained in anatomically modern humans either because it was still fitness beneficial or fitness neutral.

That quick ejaculation is now a source of distress in modern men may reflect novel expectations about men's sexual performance and women's enjoyment and desires during sex. This is not inherently bad—that women's preferences and sexual satisfaction are valued represents societal progress toward equality between the sexes. But the unavoidable consequence of women's sexual experiences mattering is a shift in expectations regarding men's sexual performance, one component of which may be time between intromission and ejaculation. Divining humans' future evolutionary trajectory is practically unfeasible, but one interesting possibility is that faster ejaculation could become selected against if it impedes men's ability to attract and maintain sexual partners.

Debates surrounding the diagnosis and treatment of premature ejaculation do reflect scientists' and practitioners' awareness that rapid ejaculation may be a typical feature of male sexual functioning. The most recent update of the diagnostic criteria for premature ejaculation in the *Diagnostic and Statistical Manual of Mental Disorders* (DSM-5) included adding a specific time constraint —ejaculation under one minute from penetration (American Psychiatric Association, 2013). Prior to this update, studies showed that many men diagnosed with premature ejaculation displayed intravaginal ejaculatory latency times that were within the typical range of times measured in men not diagnosed with premature ejaculation. Discussions preceding the update also included whether or not the term "premature" was even appropriate (Segraves, 2010). However, these considerations have been based largely on evidence related to biological and normative functioning, not evolutionary origins.

Evolutionary mismatch does not exclusively produce outcomes that are distressing or negatively impact fitness. Erectile dysfunction and age-related declines in male sexual functioning are circumstances where evolutionary mismatch, specifically modern technology, stands to improve people's experiences and may reduce sex-related dysfunction or dissatisfaction. Viagra, and other medical interventions that treat erectile dysfunction, have been

demonstrated to improve the sexual satisfaction of both men and their partners (Lewis et al., 2001; Montosori & Althof, 2004). And to the extent that erectile dysfunction reduces reproductive success, technology that extends men's reproductive capabilities could be fitness beneficial.

Sexual dysfunction in women can also be better understood through the lens of evolutionary mismatch. Lack of sexual interest is one of the most commonly reported sex problems among women (Laumann et al., 2009). The associated diagnosis in the DSM-5 is female sexual interest/arousal disorder, and symptoms sufficient to warrant diagnosis include absent or reduced interest in sexual activity, absent or reduced sexual thoughts and fantasies, and no or reduced initiation of sexual activity, all of which must cause clinically significant distress (American Psychiatric Association, 2013). There are times where low sexual motivation in women could have been fitness beneficial. As the sex incurring the greater obligatory parental investment, women would have benefited from exhibiting greater choosiness about their partners, and when to have sex, compared to men (Trivers, 1972). A woman's options for mates, the investment required for her current children, her health, and amount of currently available resources are factors that may have toggled the fitness costs and benefits related to pregnancy and raising a child. Low sexual motivation, rather than a sign of dysfunction, could be the functional output of adaptations responding to cues that becoming pregnant, or engaging in sexual behavior, would have been too fitness costly.

The suggestion that periodic or facultative reductions in women's sexual motivation are evolved rather than indicative of dysfunction, or cultural suppression of women's sexuality, may be perceived by some as antifeminist, or in opposition to the stance that men and women should be treated equally (Eagly & Wood, 2011; Kuhle, 2012). As a consequence, modern narratives that downplay the existence of evolved psychological sex differences could contribute to the distress women experience at their perceived "reduced" sexual motivation. In this way, evolutionary mismatch could be both a causal factor in the characterization of low sexual interest in women as dysfunction *and* it may lead to women being more likely to experience distress because their sexual motivation is phenomenologically different from men's and does not match a standard that assumes low sexual motivation is abnormal, or is the product of a patriarchal sociocultural influences.

In sum, defining and diagnosing dysfunction or abnormality in sexual arousal, and with respect to sexuality and mating behavior more broadly, require understanding what it means for psychological mechanisms to be operating normally or functioning properly. Defining typical functioning has long been an

integral part of clinical psychology; however, many descriptions of dysfunction hinge on an individual's subjective experience of distress and how their behavior affects their ability to function in the current environment (American Psychiatric Association, 2013). This is a reasonable starting point for practitioners whose ultimate goal is to help people be happier, healthier, and more successful in their relationships and goal achievement. However, anchoring definitions of normal functioning to success in the current environment has the potential to mask the underlying design of our psychological mechanisms, which were shaped by an environment differing in myriad ways from people's current environment. Furthermore, distress itself is often part of the design of adaptations. Experiencing pain, fear, and other aversive emotions motivates behavior to alleviate the distress, which ultimately could have been fitness beneficial. Integrating clinicians' concept of function with the concept of adaptations operating as designed is key (Wakefield, 2015). Furthermore, mismatched features of the current environment contribute to the output of typically functioning adaptations being distressing, and thus being labeled as dysfunction.

Mismatch and Mating Implications

The summarized research represents a small slice of the scholarship in each domain, and there are many more domains of study within human mating research. I selected these examples because they provide useful insights into why evolutionary mismatch matters in research on human mating, and how thinking related to evolutionary mismatch can be applied to specific research questions addressing human mating adaptations. Some important conclusions are as follows:

1. Evolutionary mismatch thinking can be used both to describe existing known phenomena and to test previously unstudied hypotheses about mating cognition and behavior;
2. Appreciation of evolutionary mismatch is necessary to ensure appropriate caution regarding interpretations about universal psychological design, or human nature, drawn from studies of mismatched people;
3. Interventions or policies designed to address societal ills can be better informed if we understand how evolutionary mismatch promotes or deters harmful or undesired behavior; and
4. Definitions of abnormality and dysfunction depend on understanding the evolved nature of psychological mechanisms, how they operate in an environment that differs from ancestral conditions, and how features of our modern environment shape attitudes and ideas about what is normal or functional.

Evolutionary Mismatch and Sample Diversity

Evolutionary social scientists have empirically demonstrated that much of the

research from which we make conclusions about universal features of human nature come from studies of people who are neither representative of the vast majority of living humans nor representative of past humans (Barrett, 2020a, 2020b; Henrich et al., 2010; Pollet & Saxton, 2019). Concerns about sample diversity and evolutionary mismatch overlap (Gurven & Lieberman, 2020). One consequence of a reliance on convenience samples—historically Western college students—is that our conclusions about the mind are drawn from a set of humans who developed, and are currently operating, in a homogenous set of conditions that are also representative of evolutionary mismatch. Every nascent student of the social sciences is taught that relying on convenience samples limits the degree to which findings of one study can be generalized to people who differ from those studied. However, for evolutionary social scientists, this concern deserves particular attention because their explicit goal is often to describe the underlying evolved structure of psychological mechanisms and identify universal features of human nature. That samples are unrepresentative limits the degree to which we can generalize our understanding of how the mind works. More insidiously, the use of a narrow slice of humanity, particularly people who are mismatched in important ways, may bias our conclusions about the mind, and generate programs of research built on shaky theoretical grounds (Barrett, 2020a, 2020b; Goetz et al., 2019).

Recent research on jealousy provides an example in which diversifying subjects of study provided a more complete picture of the evolved design of psychological mechanisms. Decades of prior research from an evolutionary perspective had focused on exploring robust sex differences in jealousy; in particular, men's greater upset at a partner's sexual infidelity compared to women's (Buss, 2018). Most of the research in this area has relied on samples from Western countries. However, in a recent study, Scelza et al. (2020) examined jealousy in eleven worldwide populations, including eight small-scale societies. They discovered another characteristic that explained important variation in jealous response—paternal investment. In cultures in which men are expected to invest more in their offspring, infidelity was viewed more severely, and jealous response was stronger. Scelza et al.'s (2020) investigation was built on an evolutionary analysis, but they were only able to study jealousy as a facultative response to expected paternal investment by studying a diverse set of populations that varied in cultural norms related this dimension. This study demonstrates the multifaceted importance of sample diversity. First, studying groups of people absent from previous studies on jealousy provided a robust test of the universality of sex differences in jealousy—Scelza et al. (2020) did, in fact, replicate the known sex difference in upset at sexual infidelity. But, of equal

importance, this research revealed a novel feature of jealousy mechanisms, one that would only be discoverable by studying populations whose cultural norms related to paternal investment spanned the full range of possibilities.

Sample diversity, or lack thereof, limits which design features of psychological mechanisms researchers can even study. Of greater concern, it may bias our conclusions about the underlying design of the mind. For example, Scelza and Prall (2018) questioned the long-term versus short-term partner dichotomy that has been a staple of evolutionary-based research on human mating since its introduction (Buss & Schmitt, 1993). They proposed an alternative dichotomy (formal vs. informal) that they argued better captures the nuances and functions of different types of mating relationships in humans. Scelza and Prall (2018) noted that the prevailing terminology developed largely from studies of relationships in Western samples, and they argued that this language does not adequately generalize across human cultures and may bias researchers' ideas about human mating strategies and evolved psychology. Evolutionary mismatch of samples may similarly shape the assumptions evolutionary social scientists make about the structure of psychological mechanisms (Goetz et al., 2019). Adding a metatheoretical kink, even assumptions about whether a characteristic is indicative of evolutionary mismatch, or is reflective of the typical range of possibilities to which ancestral humans were exposed, may be influenced by researchers' own evolutionary mismatch, and the ecology of the populations they typically study. Employing sound theory and a principled approach to hypothesizing about the design of the mind, including consideration of the EEA and evolutionary mismatch, provides a theory-based defense against developing a faulty model of the mind. Diversifying populations of study adds another layer of protection by providing a *methodological* foil against drawing limited, or biased, conclusions about human nature. Additionally, evolutionary mismatch thinking can guide researchers toward the import metrics on which to seek sample diversity—from materialism, access to smartphones, and population density to specific cultural norms.

Mismatch Conclusions: Obstacles and Opportunities

Evolutionary social scientists base their work on the recurrent stabilities of the ecologies of ancestral humans. Thinking about evolutionary mismatch requires a 180-degree shift in focus to the modern, novel, and often fleeting characteristics of the here and now. As the pace of technological advancement increases, so does the potential for evolutionary mismatch. Even some of the

specific mismatch features highlighted in this chapter, from smartphones to Viagra, will likely be replaced by other technologies in the coming decades that may interact differently with our evolved psychology. The transient nature of mismatch and its effects is part of the challenge for researchers whose training and focus lies in thinking about the regularities of the past.

At the same time, evolutionary social scientists are exclusively equipped to grapple with the concept of evolutionary mismatch and its effects because of their deep knowledge of the process of evolution, their engagement in cross-cultural research, and the breadth of methodological tools employed by the discipline. I have reviewed examples of recent work on human mating in which researchers have derived their research questions and hypotheses by explicitly thinking about evolutionary mismatch to successful ends. Evolutionary mismatch effects permeate all domains of human mating, including attraction, arousal, dysfunction, intrasexual competition, and sexual conflict. Evolutionary mismatch provides unique explanatory power in understanding some harmful or undesirable mating-related behavior, and in ascertaining when mating psychology or behavior is abnormal or dysfunctional. And this power can be leveraged to improve people's lives and happiness (van Vugt et al., 2020). But a focus on evolutionary mismatch is also necessary to develop our understanding of the design features of mating mechanisms across domains and to protect against drawing inaccurate conclusions from our studies of mismatched people. Thus, capitalizing on knowledge of the EEA of adaptations and evolutionary mismatch will advance a deeper understanding of human mating and human nature.

Note

1. However, there is current disagreement about whether life history theory does predict that species, or organisms within a species, should be characterized according to a slow–fast continuum and the extent to which available data supports the fast-slow continuum concept (e.g., Frankenhuis & Nettle, 2020).

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